

THE FUNCTION OF ZIGZAG DEFLEXIONS IN THE COMMISSURES OF FOSSIL BRACHIOPODS

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ABSTRACT. The commissures and valve-edges of many fossil brachiopods are deflected into a zigzag form. During ontogeny, this often produced radial ribs (costae) on the shell. Schmidt's hypothesis, that zigzag valve-edges acted as protective devices by transforming the apertures into narrow zigzag slits, is extended by determining the paradigm for this function. The zigzag deflexions of fossil brachiopods approximate, often very closely, to this paradigm; they are therefore interpreted as protective devices. The nature of the 'protection' conferred is discussed in the light of observations on the physiology of living brachiopods. The gradual development of paradigmatic zigzags during the later stages of ontogeny is interpreted in terms of the increasing degree of protection required as the animal grew in size. The presence of species with zigzag deflexions does not imply any special environmental conditions. The rigid specification of the paradigm, and the existence of closely similar zigzags in fossil and living oysters, suggest the intrinsic probability that zigzags were evolved many times independently. This is confirmed extrinsically by the varied origin and development of zigzags during ontogeny, and by their scattered distribution in geological time and among the major taxonomic groups. Examples are cited from most superfamilies of the Articulata, and from horizons ranging from Middle Ordovician to Eocene.

THE taxonomy of brachiopods is confused, and their evolutionary history difficult to reconstruct. This is partly because many structural features recur in taxa that seem on other criteria to be only distantly related. An analysis of the probable function of these features may help to clarify the nature and patterns of evolutionary change in the Brachiopoda.

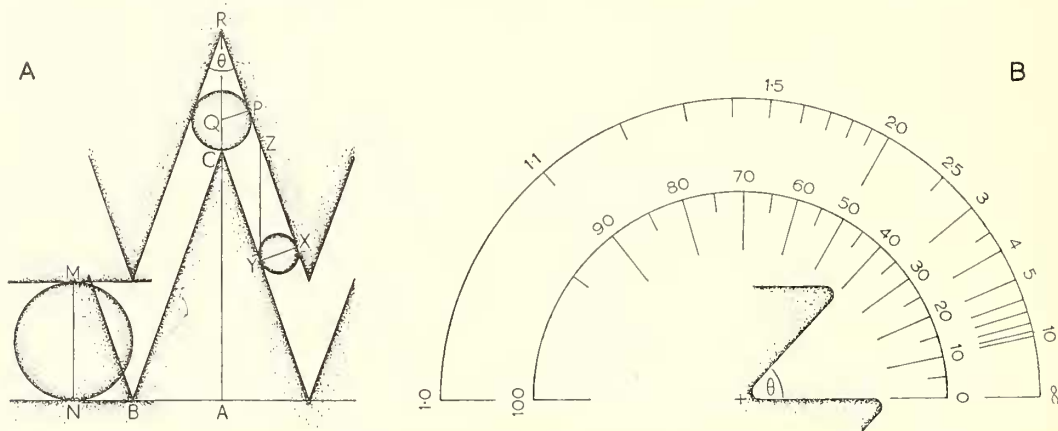
One character which occurs frequently but sporadically throughout the phylum—and indeed outside it—is a sharply angular type of radial ribbing on the surface of the shell. Causally, this is due to a special pattern of accretionary growth rates at the edges of the valves. A series of anomalies in the growth rates, predominantly in their vertical components (Rudwick 1959, p. 4), produces a *zigzag serial deflexion* at the commissure. During the further growth of the shell, a corresponding series of angular radial ribs or *costae* may be formed on the surfaces of the valves. But the prominence of these costae depends not only on the form of the deflexion, but also on the degree of overall convexity in the valves and the point in ontogeny at which the deflexion first appears. Consequently, the primary function of this character must be sought in the zigzag deflexion, rather than in the angular costae that it may or may not produce on the surface of the shell. It has been suggested, for example, that by corrugating the surface of the shell the costae may have served to increase either its mechanical strength (e.g. Cooper 1937, p. 40) or the area of the mantle tissue lining it internally (e.g. Cumings 1903, p. 131). Some costae on some shells may have had these effects, but perhaps only fortuitously; for interpretations of this kind cannot be applied to all zigzag deflexions, since some occur without any appreciable corrugation of the shell (see Pl. 27, figs. 1, 2).

The methodology of functional interpretations of fossils has been analysed elsewhere (Rudwick 1961a, p. 450; 1964). This paper follows the same method: first, the demands of a postulated function are analysed; from this analysis is derived a structural specification (the *paradigm*) which would give maximal efficiency for the function;

finally, the functional interpretation is tested by comparing this specification with the observed structure of actual fossil specimens.

THEORY OF PROTECTIVE NARROW SLITS

Many years ago, Dr. Herta Schmidt (1937, pp. 27–30) interpreted the zigzag deflexion of the rhynchonellacean *Sphaerirhynchia* (= *Wilsonia*) as a protective device. (A similar suggestion for the orthacean *Platystrophia* was made by Cumings as early as 1903, p. 131.) If the valves gaped only slightly apart, a narrow zigzag slit would have appeared between them. This slit might have prevented harmfully large particles from entering the mantle cavity. Schmidt analysed the degree of protection which a zigzag slit could

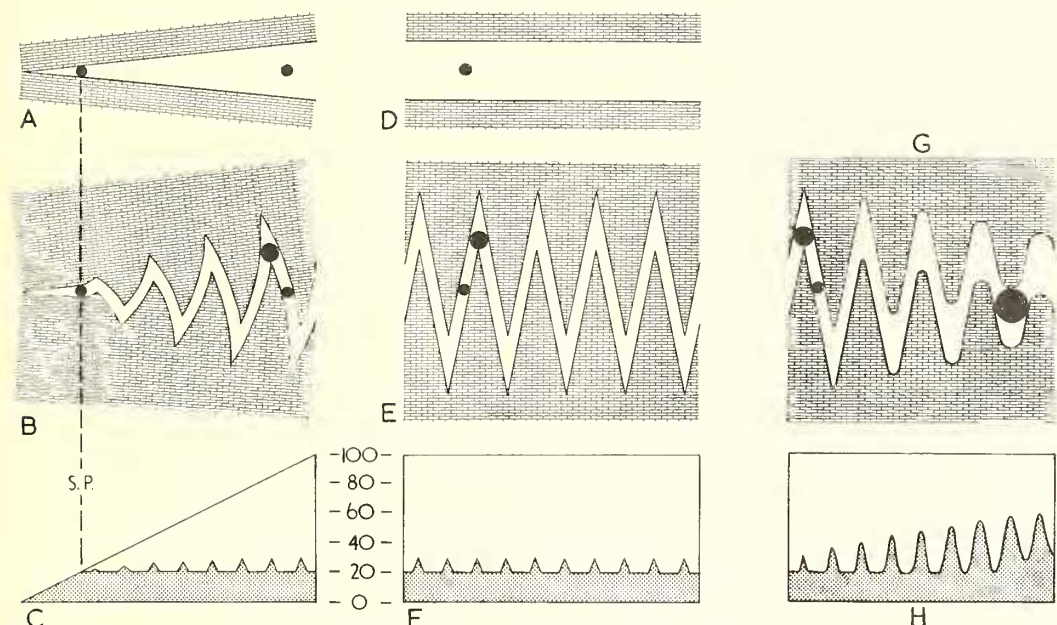


TEXT-FIG. 1. A, Portion of 'ideal' protective zigzag slit, showing spherical 'particles' passing through flanks of slit (diameter XY), crest of slit (diameter PQ), and undeflected slit of same gape (diameter MN). Degree of protection of slit, $P = 3.0$; width of slit = 33 per cent. of gape; crestal angle = 39° . B, Protractor for determining degree of protection (outer circle), and width of slit as percentage of gape (inner circle), from crestal angle of zigzag. A zigzag is shown in position for measurement ($P = 2.5$ or slit = 40 per cent.).

give at three different degrees of opening of the shell, treating the 'harmful particles' under the ideal form of small spheres (Schmidt, Abb. 12). The zigzag deflexion could confer a functional advantage relative to an undeflected commissure, either by increasing the area of the slit without increasing the risk of entry of harmful particles, or by reducing that risk without reducing the area. If the advantage is expressed as a ratio between the deflected and undeflected conditions, Schmidt's three alternatives become identical.

Let the valve edges separate through a vertical distance to be termed the *gape* (text-fig. 1A, $YZ = CR$). For a unit length of the commissure, this determines the area of the slit. Let the *relative amplitude* of the zigzag be the ratio between the length of its *flank* and half the 'wavelength' between adjacent *crests* (i.e. BC/AB). Let the *degree of protection* (P) of the zigzag slit be expressed as the ratio (MN/XY) between the diameters of (a) the largest sphere able to pass through an undeflected slit of the same area (MN), and (b) the largest particle able to pass through the flanks of the zigzag slit (XY). Then the degree of protection is equal to the relative amplitude ($MN/XY = YZ/XY = BC/AB$, by similar triangles XYZ , ABC). Therefore the degree of protection depends only on the

'strength' of the zigzag, and not on the extent to which the valve edges gape apart; it can therefore be determined even for fossil brachiopods. The width of the zigzag slit may be expressed as a fraction of the width of the undeflected slit (XY/MN or $\sin \theta/2$), i.e. the reciprocal of the degree of protection.



TEXT-FIG. 2. Paradigm for protective zigzag slits. A, D, Undeflected valve edges perpendicular and parallel to hinge-axis. B, E, Valve edges with corresponding paradigmatic zigzag deflexions, gaping apart to same degree; S.P., suppression point. C, F, Graphs showing maximum size of particle admitted at each point of zigzags, relative to maximum gape (= 100 per cent.): particles up to 30 per cent. at crests, but uniform at 20 per cent. on flanks; degree of protection $P = 5.0$. G, H, Effect of angular and rounded crests on protective efficiency of zigzag slit ($P = 5.0$); G, slit with crests of varying degrees of angulation; H, corresponding graph showing maximum size of particle admitted at each point.

For any given zigzag there is a constant ratio between the diameters of the largest particles able to pass through the crests and the flanks of the slit (by similar triangles PQR , XYZ). The particles passing through the crests are in fact localized anomalies in an otherwise uniform degree of protection, represented by the particles passing through the flanks (text-fig. 2F). This justifies using the latter, i.e. the width of the slit, for defining the 'degree of protection'.

An ideal deflexion must give a zigzag slit which is uniformly narrow at all points, and in which the deleterious effect of the crests (in allowing the passage of particles larger than the rest of the slit) is reduced as much as possible. This is ensured by a deflexion of uniformly high relative amplitude and large wavelength, with uniformly inclined flanks (text-fig. 2D, E), and sharp crests (text-fig. 2G, H).

But this specification presupposes portions of the valve edges which, when gaping apart, are equidistant from one another at all points (text-fig. 2D, E). In an actual brachiopod this condition would be approached most closely on an arc parallel to the hinge-axis (i.e. usually the antero-median arc). But even here, since the valve edges separate, not on a linear course, but by rotation around the hinge-axis, the zigzag

deflexion must be an *axial deflexion* (Rudwick 1959, p. 13), lying in a cylindrical surface centred on the hinge-axis (text-fig. 3A).

For a zigzag slit which lies in a plane perpendicular to the hinge-axis, the relative amplitude must decrease in a definite '*graded*' way towards the hinge-axis ($\sin \theta/2 \propto 1/a$, where a is the distance from the hinge-axis). At one particular *suppression point* (S.P.), the relative amplitude will fall to unity ($\theta = 180^\circ$), and the zigzag deflexion will therefore die away (text-fig. 2A-C). Between the suppression point and the hinge-axis the commissure will be undeflected, and the slit necessarily less than the standard width. The flanks of the zigzag will be curved, with the concave side of each flank facing the hinge-axis (text-fig. 2B); this is due partly to the continuously changing angle of inclination required for a slit of uniform width, and partly to the fact that the valve edges move apart by rotation. As in a deflexion parallel to the hinge-axis, the deleterious effect of the crests will be reduced by a zigzag that is sharp-crested and of large wavelength.

In actual brachiopods, since most of the commissure is curved in plan and inclined obliquely to the hinge-axis, the paradigm for a protective zigzag deflexion will combine these specifications. It will be (a) axial, (b) sharp-crested, (c) of large relative wavelength, i.e. of low *crestal number* (N , the total number of crests distinguishable around the commissure), (d) of high relative amplitude and straight flanks anteriorly, and (e) of appropriately graded relative amplitude and flank-curvature laterally and posteriorly. Such a deflexion will produce a *graded zigzag slit* (text-fig. 3B, C) of uniform width all round the commissure, from one suppression point round to the other. It can be shown graphically by plotting the relative width of the slit at each point. The relative gape (directly proportional to the relative distance from the hinge-axis) gives a *gape curve*. The width of the slit (derived from the relative amplitude and gape at each point) gives a *slit curve*. If the zigzag is perfectly graded, the slit curve will be a horizontal straight line, intersecting the gape curve at the suppression points. The proximity of the slit curve to the base line indicates the degree of protection given by the zigzag. (Each point on a slit curve represents the mean between the widths of the slit on either side of each crest, though intermediate points can be determined if necessary; the slit curve does not show the effect of the crests themselves.)

Grading ensures that the slit on all arcs of the commissure is as wide as possible, without detracting from the degree of protection given. This would minimize the extra resistance to the flow of water through the gape, caused by drag against the lengthened edges of the valves. Any zigzag must be a compromise between protection and rate of flow.

ZIGZAG DEFLEXIONS IN FOSSIL BRACHIOPODS

Material studied. In this section, the interpretation of zigzag slits as protective devices is tested by comparing the functional paradigm with the actual deflexions of fossil brachiopods.

Although I have searched several large collections, the species cited or figured here (see list in Appendix) are not an accurately representative sample of all species with zigzags. The faunas of some periods, particularly the Triassic and Upper Carboniferous, are certainly under-represented; and in some instances I have had to rely on published figures. The available faunas of some other periods, particularly the Jurassic, have been so abundant that the sample is probably overweighted at these points. Moreover, the

faunas of different periods have received very unequal attention from modern systematists; as Cooper and Williams (1952) showed in another context, quantitative conclusions cannot safely be drawn from data of this kind (see also Williams 1957). But I believe that the coverage has been complete enough to show qualitatively the pattern of distribution of zigzag deflexions.

The repositories of the figured specimens are shown by the following abbreviations: A.M.N.H., American Museum of Natural History, New York; C.M.Z., Cambridge University, Museum of Zoology; M.C.Z., Museum of Comparative Zoology, Harvard University; S.M., Sedgwick Museum, Cambridge University; U.S.N.M., United States National Museum, Washington; U.W.I.P., Universität von Wien, Institut für Paläontologie.

Techniques for the analysis of zigzag deflexions. The presence of grading is shown by the regular reduction in amplitude towards the hinge, and the curvature of the flanks of the zigzag. The degree of grading can be estimated fairly simply: if a comparison with a chart of zigzags of known amplitude shows that the width of the slit anteriorly is 20 per cent. of the gape, then the suppression points for perfect grading will be 20 per cent. of the distance between the hinge-axis and the front of the shell (text-fig. 3A, C). (Determinations from published figures are obviously less reliable, since it cannot be assumed that 'lateral views' are in fact strictly lateral.) A more accurate analysis of the grading can be made by constructing a slit curve. Though somewhat laborious, this is greatly simplified in practice by the use of a specially calibrated protractor (text-fig. 1B), which gives the width of the slit or the degree of protection directly from the crestal angle; and by the use of other graphical devices which convert the positions of the crests directly into percentage distances, and allow the points on the slit curve to be plotted without any actual numerical calculation.

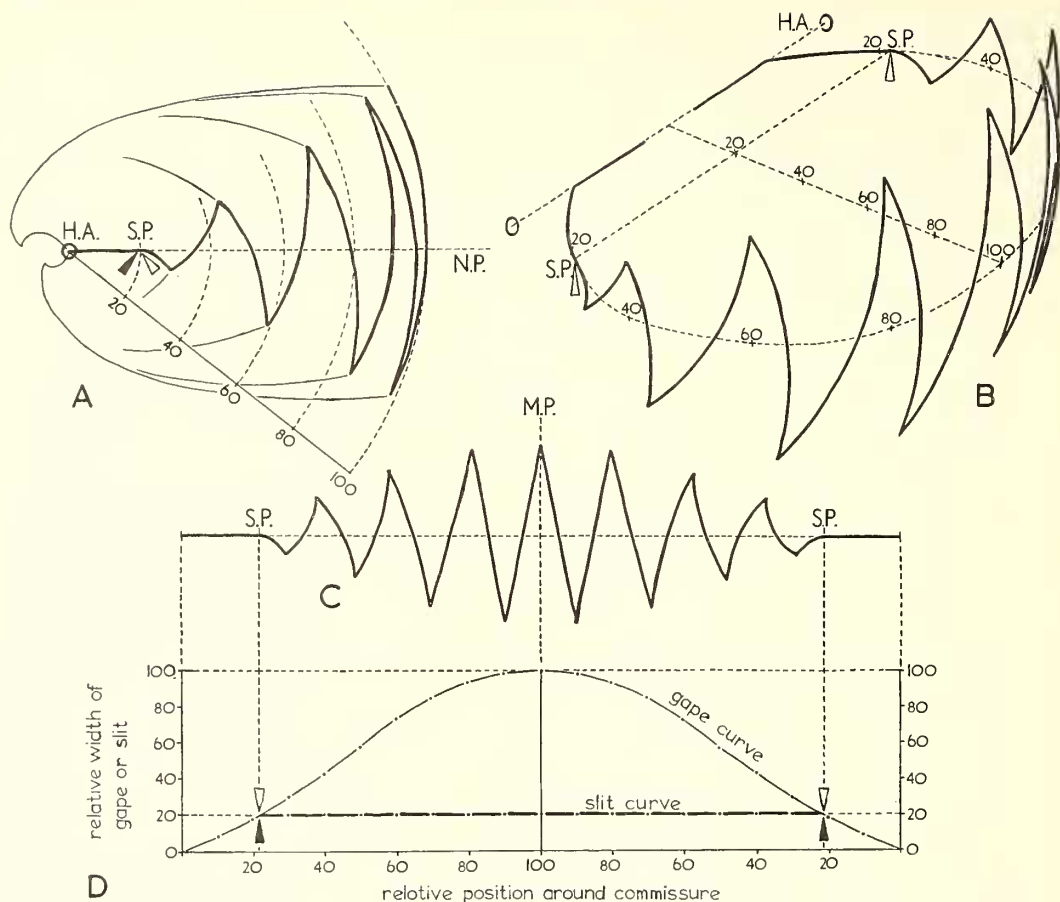
Note on illustrations. Most zigzag deflexions are illustrated in the text-figures by standard anterior and lateral views of the shell, traced from photographs. The dorsal valve is always shown uppermost. The lines marked on the valve surfaces are the loci of crests of the zigzag. In the *lateral view*, the normal plane (where distinguishable) is indicated by a small arrow pointing towards the shell; the orientation of the median deflexion (if present) is shown by a small arrow pointing away from the shell; a small circle marks the hinge-axis. An open and a black isosceles triangle point to the actual and ideal suppression points respectively. On the *anterior view*, a vertical line indicates the median plane; a horizontal line ending in two small circles shows the position of the hinge-axis projected into the plane of the drawing. *Commissure traces* and *slit curves* may also be given, but they are not drawn to scale. All the photographs reproduced here were taken after coating thinly with ammonium chloride. They are oriented with the dorsal or adapical direction (as appropriate) uppermost.

Classification of zigzag deflexions

Since brachiopod shells grow by accretion and leave traces (in the growth-lines) of the stages of their growth, the genesis of a zigzag deflexion can be described from any well-preserved specimen. This provides the basis for a classification of the deflexions, for their origin and development during ontogeny are remarkably diverse. In the ontogenetic descriptions which follow, terms such as 'early', 'late', 'slow', and 'rapid' refer not to the absolute time-scale of growth (which is of course unknown in fossil species), but to the relative time-scale provided by the growth in the overall size of the shell. The reference throughout is to ontogeny, not to phylogeny.

In distinguishing different types of zigzag, an attempt is made to translate the definitions into 'cumulative' terms of description; but since the cumulative expression of the deflexions (i.e. in costae, folds, sulci, &c.) depends on the individual shell form, these 'translations' can only be approximate.

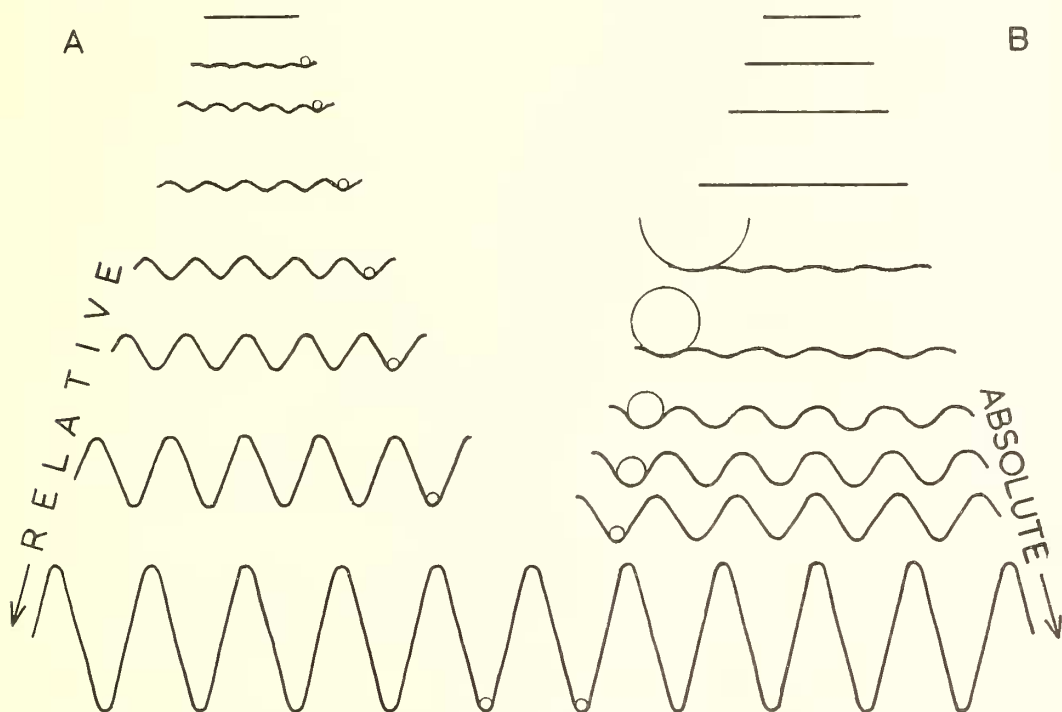
All zigzag deflexions were formed during ontogeny by the modification of an earlier



TEXT-FIG. 3. Paradigm for protective zigzag deflexion ($P = 5.0$) on commissure of subcircular plan. A, Lateral view of shell; note curvature of anterior commissure in arc centred on hinge-axis (H.A.)—definitive of an *axial* deflexion; note suppression point (S.P.) at 20 per cent. of distance from hinge-axis—since deflexion is paradigmatic, actual suppression point (white pointer) coincides with ideal (black pointer); N.P., normal plane; (N.B. this is only one possible form of shell on which this commissure could occur). B, Perspective view of commissure; numerals show (i) percentage perpendicular distances from hinge-axis towards anterior side, and (ii) percentage distances from hinge-line around projection of commissure into normal plane; note curvature of flanks of zigzag. C, Commissure trace, reduced. M.P., median plane; compare median and lateral arcs with text-fig. 2E, B, respectively. D, Gape curve and slit curve for the commissure; vertical and horizontal axes calibrated from B with numerals (i) and (ii) respectively; horizontal slit curve, at 20 per cent. on vertical axis, implies perfect grading with degree of protection = 5.0; compare median and lateral portions with text-fig. 2F, C, respectively.

serial deflexion of more rounded or *undulate* form. This *angulation* (text-fig. 4) may be either relative or absolute. In *relative angulation*, the undulate deflexion arose early in ontogeny, and thereafter became gradually more angulate: as the wavelength increased the flanks became longer and straighter; but the crests, although becoming relatively sharper, maintained a constant absolute degree of rounding (text-fig. 4A). In *absolute angulation* the deflexion remained undulate until a fairly late stage; the crests then became sharper absolutely (i.e. their minimum radius of curvature decreased) while the

flanks were becoming straighter (text-fig. 4B). The final zigzags produced by these two processes may be indistinguishable. In most shells the angulation can be confidently assigned to one class or the other by simple inspection of the growth-lines; in a few the evidence is more ambiguous, so that this distinction cannot be regarded as entirely rigid.



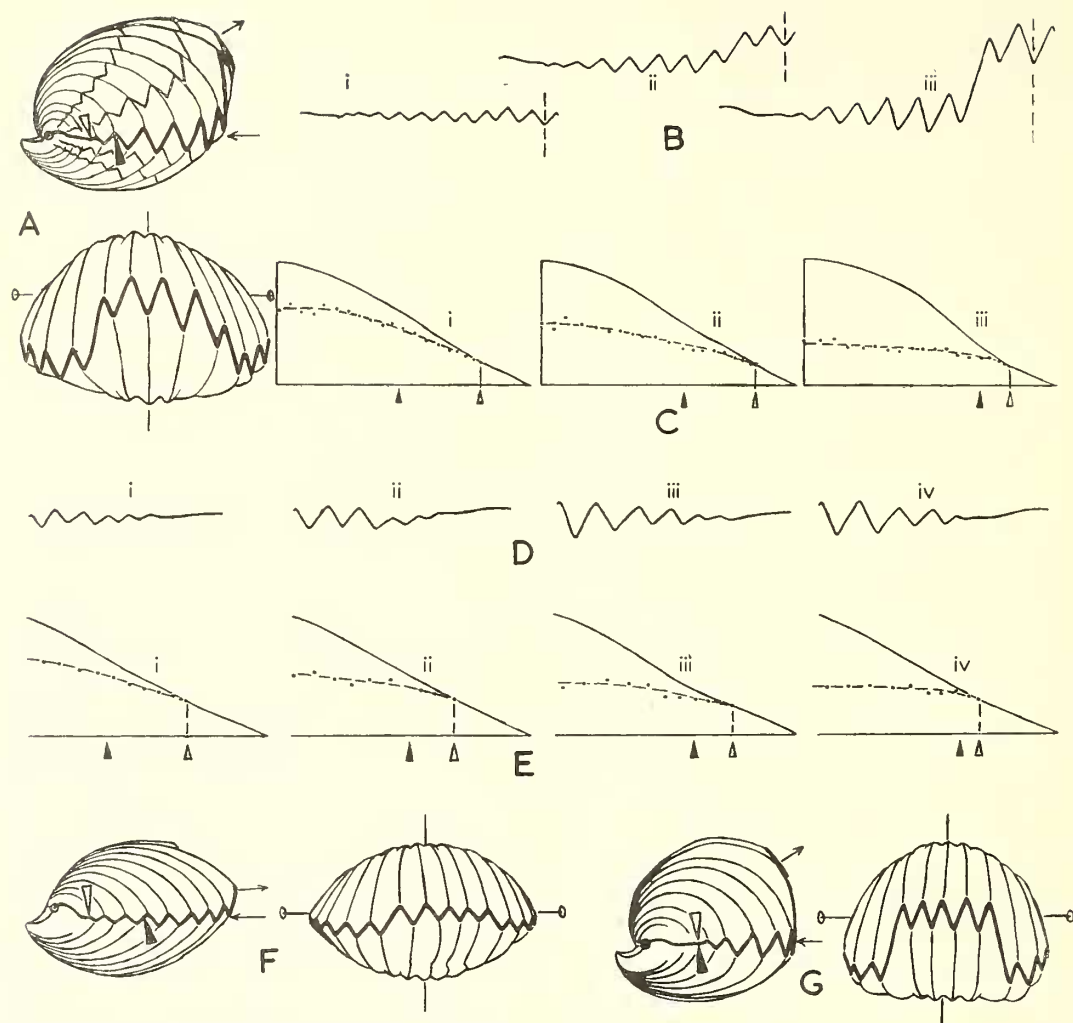
TEXT-FIG. 4. Diagram to show formation of zigzag deflexion during ontogeny by relative (A) or absolute (B) angulation of a pre-existing undulate serial deflexion. Each line represents the same (anterior) arc of the commissure, growing in length during ontogeny. The circles fitted into certain crests show the radius of curvature of the crests—almost constant during relative angulation, rapidly reduced during absolute angulation.

Group A

The serial deflexion from which the zigzag was ultimately produced arose very early in ontogeny, and appeared almost simultaneously on all arcs of the commissure. (In cumulative terms, all the costae arise close to the umbo of each valve.)

Subgroup A. I (text-figs. 5–7; Pls. 21–24): The crestal number remained almost constant after an early stage in ontogeny, and the zigzag was produced by relative angulation. (In cumulative terms, most of the costae extend without interruption from near the umbo to the commissure, becoming gradually broader and relatively more sharply ridged.)

This subgroup contains a wide variety of shells: *Globirhynchia* may be taken as an example (text-fig. 5; Pl. 21, figs. 6, 7; Pl. 22, figs. 3–5). Relative angulation gave the deflection a zigzag form at a fairly early stage; but its relative amplitude was low, and



TEXT-FIG. 5. Zigzags of Subgroup A. I: Rhynchonellacea: *Globirhynchia*. A, 'Adult' shell of *G. subobsoleta* (Davidson): right lateral and anterior views; $P = 3.0$; $N = 32$; grading good; median deflexion slightly asymmetrical. S.M. J. 48763, $\times 1.5$. B, Three stages in growth of right half of commissure of same shell; note progressive suppression of crests. C, Slit curves for same growth stages; note approach towards perfect grading; final degree of protection = 3.0 . D, Four stages in growth of lateral arc of commissure of another shell; note progressive suppression of crests. S.M. J. 48766. E, Slit curves for same growth stages; note approach towards perfect grading; final degree of protection = 2.5 . F, 'Young' shell with poor grading and weak median deflexion; $P = 2.0$; $N = 38$. S.M. J. 48767, $\times 3$. G, 'Adult' shell of *G. tatei* (Davidson): $P = 3.0$; $N = 28$; grading perfect; deep median deflexion with steepened flanks. S.M. J. 48761, $\times 3$. All from Oolite Marl, Inferior Oolite (M. Jurassic); Notgrove Station (A-F) and The Frith quarry, Painswick (G), Gloucestershire, England.

also fairly uniform on all arcs of the commissure. Consequently the degree of protection was low and the grading poor (text-fig. 5F; Pl. 21, fig. 7). In later stages the relative amplitude on the more anterior arcs rose rapidly. This not only increased the overall degree of protection, but also, by shifting the ideal suppression point towards the hinge, tended to improve the grading. Moreover, at the same time the crests nearest the hinge were gradually and progressively suppressed, so that the actual suppression point was shifted forwards towards the ideal. This *crestal suppression* can easily be detected in the growth-lines on the postero-lateral sectors of the valve-surfaces (Pl. 22, figs. 3, 5); and its effects can be determined by tracing successive growth-lines and analysing their slit-curves (text-fig. 5B-E). Thus the final commissure of a 'mature' specimen may have a moderately high degree of protection and good grading (text-fig. 5A; Pl. 21, fig. 6). A complication is introduced by the development of a dorsal median deflexion, which was superimposed on the much earlier serial deflexion. At first the median deflexion was very weak; it merely shifted the antero-median arc of the zigzag very slightly in a dorsal direction, and lengthened two of its flanks (text-fig. 5F). As the median deflexion increased in height, its lateral flanks either coincided with a single flank of the zigzag (text-fig. 5B; Pl. 22, fig. 4) or else were 'shared' by more than one flank of the zigzag. Since the median deflexion was often slightly asymmetrical, both these conditions may be found in a single shell (text-fig. 5A). The median deflexion did not affect the degree of protection of the zigzag, and is therefore not apparent in the slit-curves (text-fig. 5C).

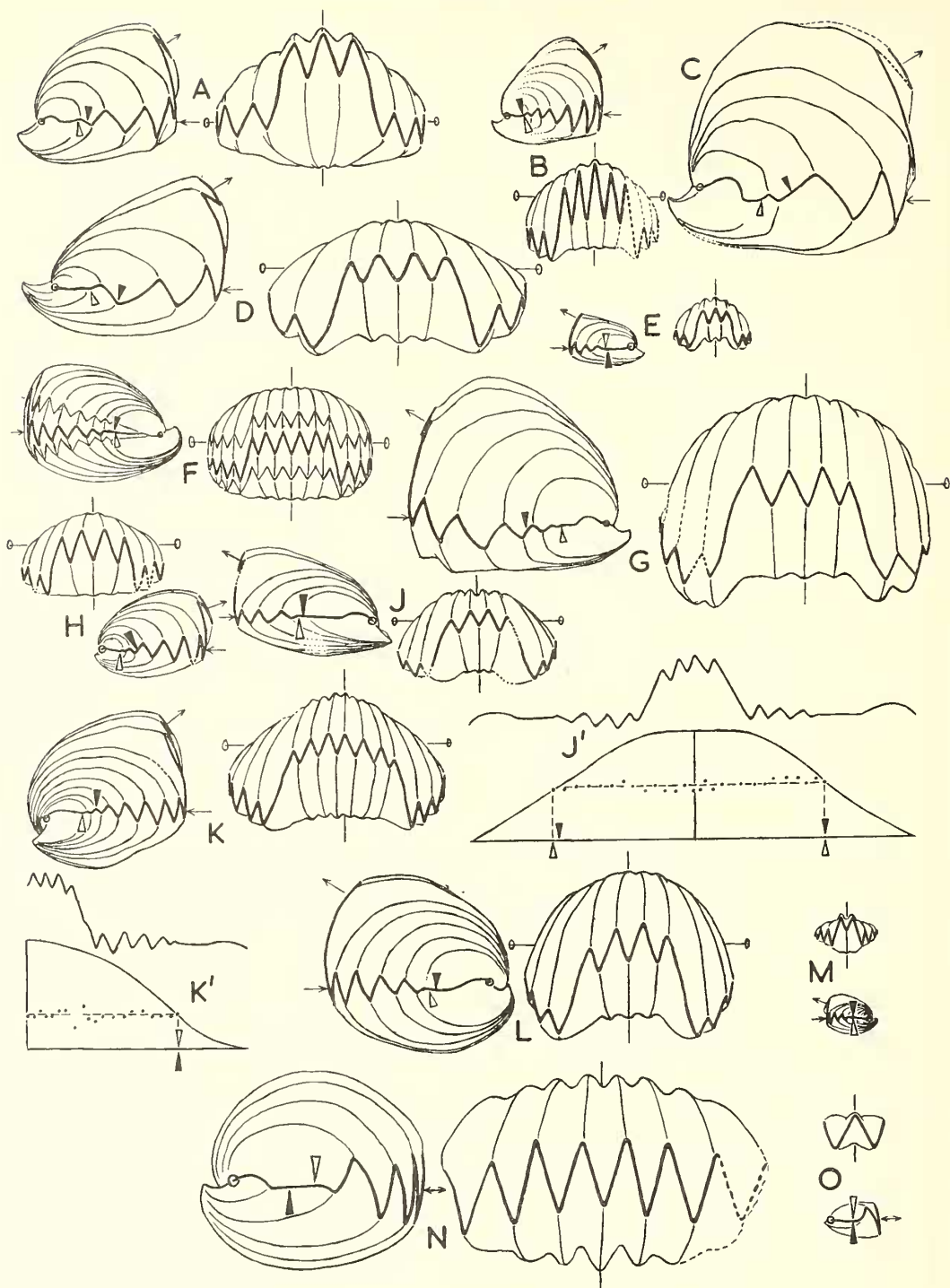
Even within the single genus *Globirhynchia*, there is great variation in the absolute size at which a zigzag with a given degree of protection may be found. Thus a typical mature specimen of *G. tatei* (text-fig. 5G) has a well-graded zigzag similar in form to that of a typical specimen of *G. subobsoleta* (text-fig. 5A), although it is only half as large in linear dimensions.

Similar zigzags are abundant among the rhynchonellaceans of every period from the Ordovician (in which the superfamily first appeared) until the Cretaceous (text-fig. 6; Pls. 21-23), and they also occur sporadically in several other superfamilies (text-fig. 7; Pls. 23-24).

The serial deflexion always arose early in ontogeny. Its crestal number was usually fairly high, but very exceptionally as low as five (text-fig. 6O). Occasionally its initial crestal number was increased at an early stage by the production of new crests (i.e. new costae appear near the umbo: Pl. 24, fig. 4). The ridges of the costae show that the angulation was predominantly relative (Pl. 21, figs. 4, 5; Pl. 23, figs. 1, 4, 6, 8; Pl. 24, figs. 4, 5).

The zigzag might at first be poorly graded (text-fig. 7H), but was generally improved in the final stages by posterior crestal suppression (text-fig. 7J; Pl. 23, fig. 6; see also Pl. 23, figs. 2, 7; Pl. 24, figs. 3, 5). Where such suppression failed to occur, the posterior part of the deflexion, behind the ideal suppression point, sometimes retained its much earlier undulate form (Pl. 23, fig. 3). On 'mature' shells the zigzags often approximated closely to the paradigm: anteriorly they had straight flanks and uniform amplitude (Pl. 22, figs. 1, 6; Pl. 24, fig. 8) and the degree of protection was sometimes very high (Pl. 21, fig. 2); while laterally the flanks were appropriately curved and graded in amplitude (Pl. 21, fig. 2; Pl. 23, figs. 1, 4).

Usually there is a dorsal median deflexion. It invariably appeared later than the serial deflexion, and merely shifted the antero-median arc of the commissure in a dorsal

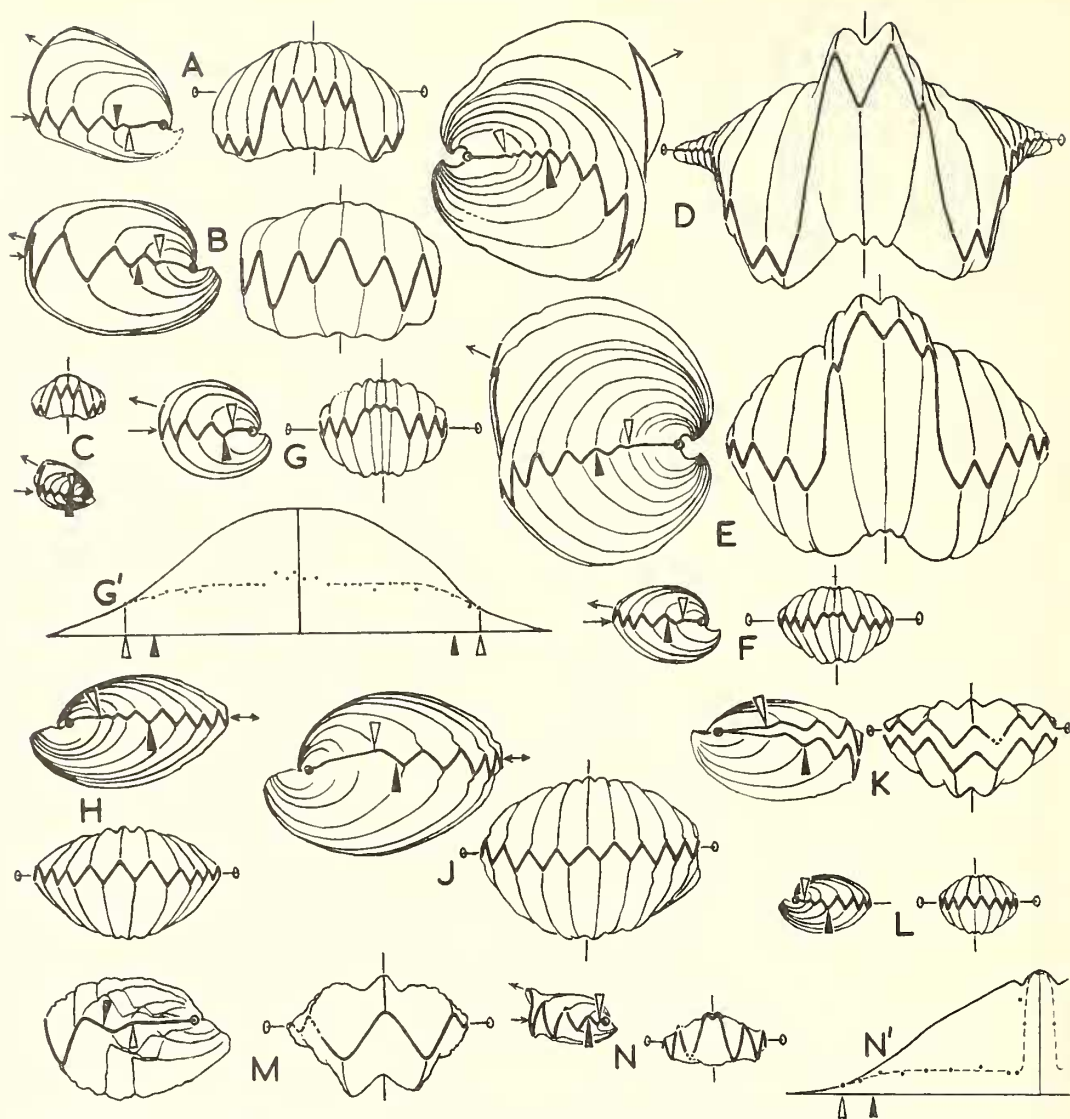


TEXT-FIG. 6

direction. Occasionally this arc was distinguished from the lateral arcs, even at an early stage, by the production of new crests of the serial deflexion (in cumulative terms, there is some 'branching' of the costae in the median sector near the umbo, Pl. 21, fig. 1). The number of crests of the serial deflexion incorporated in the median deflexion is highly variable, even, sometimes, within a single species: in some species there were as few as three crests there (text-figs. 6M, 7N; in cumulative terms, there are only two costae on the fold and one in the sulcus). The quality of the putative protection of the median deflexion is generally exactly the same as that of the lateral arcs, so that the presence of the median deflexion is not apparent on the slit-curves (text-fig. 6J', K'). But in some shells the protection of the antero-median arc was distinctly poorer than that of the lateral arcs, for example, by having a lower amplitude or lower wavelength or poorer angulation of the crests (text-figs. 6D, 7B, F, G, N; Pl. 24, fig. 1). Even on the flanks of the median deflexion the width of the slit was either unaltered or only reduced in the final growth stages by a relative steepening (text-figs. 6A-M, 7A-G). Occasionally this steepening involved the reduction or even elimination of some flanks and crests of the zigzag (in cumulative terms, costae on the flanks of the median fold or sulcus may be reduced or even die out towards the commissure: Pl. 21, fig. 3; pl. 22, fig. 1; Pl. 23, fig. 5; Pl. 24, fig. 2). In a few shells the zigzag deflexion was unaffected by any median deflexion whatever (text-figs. 6N, O; 7H-M).

Occasional specimens are preserved with the valves gaping slightly apart; these demonstrate clearly the zigzag slits that the deflexions would have produced (Pl. 21, figs. 8, 9, 12).

TEXT-FIG. 6. Zigzags of Subgroup A. I (except B, Subgroup B. I): Rhynchonellacea. All $\times 1.5$ (except N, $\times 1$). A, '*Rhynchonella* *walkeri* Davidson. P = 3.0; N = 20; grading almost perfect. Claxby Ironstone (L. Cretaceous); Claxby, Lincolnshire, England. S.M. B. 11401 (figured Davidson 1874, pl. viii, fig. 33). B, '*Rhynchonella* *personata* von Buch (?). P = 7.5; N = c. 35; grading perfect. 'M. Callovien' (U. Jurassic); 'Elatma, gouv. de Tambow' [Tambov], Russia. S.M. F. 9722. C, *Russirhynchia* *fischeri* (d'Orbigny). P = 2.5; N = 19; grading fair. 'L. Portlandien' (U. Jurassic); Mniovniki, near Moscow, Russia. S.M. F. 9671. D, '*Rhynchonella* *subvariabilis* Davidson. P = 2.5 (less in median deflexion); N = 20; grading fair on lateral arcs. Kimeridge Clay (U. Jurassic); Wheatley, Oxfordshire, England. S.M. J. 1506. E, '*Rhynchonella* *decurtata* Girard. P = 2.5; N = c. 17; grading perfect (?). 'Muschelkalk' (M. Trias); Recoaro, Vicenza, Italy. (After Bittner 1890, Taf. 32, fig. 3.) F, *Uncinunellina* *jabiensis* (Waagen). P = 3.0; N = 35; grading perfect; note vertical zones between marked growth-line and final commissure. U. Permian; Basleo, Timor. S.M. A. 11512. G, *Camarotoechia* *pleurodon* (Phillips). P = 2.5; N = 33; grading fair. Gastropod beds, Carboniferous Limestone (L. Carboniferous); Ashfell Edge, Westmorland, England. S.M. E. 10425. H, *Stegerhynchus* *daphne* (Barrande). P = 3.2; N = 29; grading fair. Kopanina limestone (U. Silurian); 'Jarow', Czechoslovakia. S.M. A. 50252. I, J, '*Rhynchotrete* *cuneata* (Dalman). P = 2.0; N = 22; grading perfect. M. Silurian; Klinte, Gotland, Sweden. S.M. A. 8779 (figured St. Joseph 1937, text-fig. 6). K, K', *Camarotoechia* *borealis* (Schlotheim). P = 3.0; N = 40; grading good. Wenlock limestone (M. Silurian); Dudley, Worcestershire, England. K, S.M. A. 8709; K', S.M. A. 8682. L, *Lepidocyclus* *capax* (Conrad). P = 3.0; N = 25; grading perfect. 'Hudson River group' (U. Ordovician); Ohio. S.M. A. 47252. M, *Rostricellula* ? *minuta* Cooper. P = 3.0; N = 23; grading perfect. L. Hermitage formation (M. Ordovician); near Woodbury, Tennessee. (After Cooper 1956, pl. 137, figs. 1, 3.) N, *Halorella* *amphitoma* (Bronn) var. *cristagalli* Bittner. P = 3.6; N = c. 21; grading good. Kalke der Hohen Wand (U. Trias); Wiener Neustadt, Austria. (After Bittner 1890, Taf. 20, fig. 15.) $\times 1$. O, *Oligorhynchia* *angulata* Cooper. P = 2.0; N = 5; grading perfect. Hogskin member, Lincolnshire formation (M. Ordovician); Luttrell, Tennessee. (After Cooper 1956, pl. 125, figs. 42, 44.)



TEXT-FIG. 7. Zygags of Subgroup A. I: Other than Rhynchonellacea. All $\times 1.5$ (except D, $\times 2$). A, Rhynchopora: *Rhynchopora nikitini* Tschernyschew. $P = 3.0$; $N = 27$; grading good. Goniatile bed (U. Carboniferous); Pariñas Quebrada, Amotape Mts., Peru. S.M. A. 14825. B, Punctospiracea: *Hustedtia hessensis* King. $P = 2.7$; grading good; crests less angulate in median deflexion. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27328/1:1 (figured Stehli 1954, pl. 27, figs. 10, 11). C, Syntrophacea: *Plectocamara costata* Cooper. $P = 2.5$; $N = c. 21$; grading good (?). Hogskin member, Lincolnshire formation (M. Ordovician); near Washburn, Tennessee. (After Cooper 1956, pl. 122, figs. 9, 10.) D, Orthacea *Platystrophia cypha* (James). $P = 2.5$; $N = c. 37$; grading fair; waves on flanks of median deflexion almost or completely eliminated from final commissure. Arnheim formation (U. Ordovician); Summit, Mason Co., Kentucky. U.S.N.M. 78670, $\times 2$. E, Orthacea: *Platystrophia crassa* (James). $P = 2.3$; $N = 32$; grading fair—some posterior suppression; 'Hudson River group' (U. Ordovician); Cincinnati, Ohio. S.M. A. 47092. F, Athyracea: *Rhynchospirina baylei* (Davidson). $P = 2.5$; $N = 24$; grading fair; wavelength low in

Subgroup A. II (text-fig. 8; Pl. 25): The crestal number was radically reduced at a fairly late stage in ontogeny, the reconstituted deflexion undergoing relative angulation. (In cumulative terms, the fine costae which extend radially from near the umbo of each valve are replaced near the commissure by a much smaller number of broader costae.)

This is a small, but highly distinctive, group. The serial deflexion arose very early, and generally had a high crestal number (Pl. 25, figs. 1, 2, 3, 6). At a fairly later stage, after it had begun to be affected by a dorsal median deflexion, but while it was still low in relative amplitude, *crestal reduction* began to occur. This involved the rapid coalescence of groups of adjacent crests, or the suppression of some crests and the retention of others. The angularity of the initial crests was usually carried over without a break into the surviving reconstituted crests; and the new deflexion, thereafter, became a zigzag by relative angulation. Crestal reduction sometimes affected all arcs of the commissure simultaneously; but, more commonly, it occurred first on the antero-lateral arcs, just outside the median deflexion, and then spread both laterally and medially. Postero-laterally, it spread at least as far as the ideal suppression point; beyond this point a few 'unreduced' crests might persist (Pl. 25, figs. 2, 4) or might ultimately be suppressed in the usual way to give perfect grading. Occasionally the reduction failed to spread into the median deflexion, so that the median arc of the final zigzag remained anomalously low in wavelength (text-fig. 8D; Pl. 25, fig. 3). The distinctive shell-form produced by this sequence of events is confined to the rhynchonellaceans, but occurred sporadically in the Devonian, the Jurassic, and the Cretaceous.

Group B

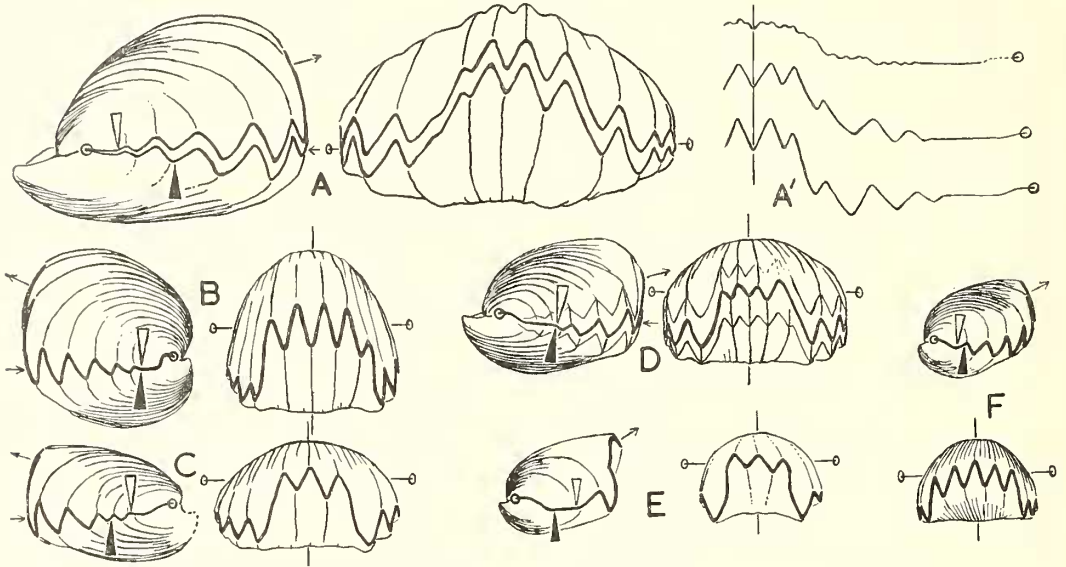
The serial deflexion from which the zigzag was ultimately produced arose progressively throughout ontogeny, spreading gradually from the anterior on to the lateral arcs of the commissure. (In cumulative terms, the medial costae arise nearer the umbo than the more lateral costae.)

Subgroup B. I (text-figs. 9, 10; Pls. 26, 27): The serial deflexion arose moderately late in ontogeny, and on the final commissure had a moderately large crestal number; it was transformed into a zigzag by predominantly absolute angulation at a late stage.

median deflexion. 'Gothland limestone series' (Silurian); Gotland, Sweden. S.M. A. 48786. G, G', Athyracea: *Trematospira salteri* (Davidson). P = 3·0; N = 23; grading good laterally; wavelength and amplitude lower in median deflexion. Wenlock Limestone (M. Silurian); Dudley, Worcestershire, England. G, S.M. A. 27189; G', S.M. A. 27182. H, J, Terebratulacea: *Eudesia cardiium* (Lamarck). H, Immature specimen; P = 2·0; N = 33; grading poor. J, Mature specimen; P = 2·0; N = 24; grading good (but with slightly lower degree of protection in median arc). Great Oolite (M. Jurassic); Minchinhampton, Gloucestershire, England. H, S.M. J. 22427; J, S.M. J. 22433. K, Terebratulacea: *Choristothyris plicata* (Say). P = 1·6; N = 13; grading fair. Navesink Marl (?) (U. Cretaceous); New Egypt, New Jersey, S.M. F. 8033. L, Punctospiracea: *Hustedia mormoni* (Marcou). P = 2·2; N = 27; grading fair. Osage group (L. Carboniferous); Howard, Kansas. S.M. E. 14947. M, Terebratulacea: *Ismenia pectunculoides* (Schlotheim). P = 1·7; N = 9; grading good. 'Jurakalk' (U. Jurassic); Nattheim, Baden, W. Germany. S.M. F. 15993. N, N', Athyracea: *Plectospira ferita* (von Buch). P = 3·5; N = 17; grading good; median deflexion not angulate; the very prominent crests are simply due to the strong zigzag developed on valves of weak overall convexity. Devonian; Eifel, W. Germany. S.M. H. 5263.

(In cumulative terms, the costae arise some distance from the umbo of each valve; near the commissure there is a moderately large number of sharply ridged costae.)

This subgroup, like Subgroup A. I, contains a wide variety of shells: *Pugnax pugnax* may be taken as an example (text-fig. 9A; Pl. 26, fig. 1). In the early stages of growth the valves were smooth (apart from very fine costellae) and the commissure rectimarginate.



TEXT-FIG. 8. Zigzags of Subgroup A. II: Rhynchonellacea. All $\times 1.5$. A, A', *Cyclothyris antidichotoma* (Buvignier). A: $P = 2.5$; $N = 29$; grading fair; shell preserved gaping. Lower Greensand (L. Cretaceous); Upware, Cambridgeshire, England. S.M. B. 25761. A': commissure traces from three successive stages. S.M. B. 25764. B, *Rimrhynchia anglica* (Rollier). $P = 4.5$; $N = 31$; grading perfect. Middle Lias (L. Jurassic); West Tynning, near Radstock, Somerset, England. S.M. J. 36345. C, *R. anglica*. $P = 2.3$; $N = 28$; grading fair; note that waves between ideal and actual S.P. are those still unaffected by crestal reduction. Middle Lias (L. Jurassic); Cheltenham, Gloucestershire, England. S.M. J. 36867. D, *R. anglica*. $P = 2.4$; $N = 24$; grading perfect; note median arc unaffected by crestal reduction, and posterior suppression between marked growth line and final commissure. Locality as C. S.M. J. 36871. E, *Furcirhynchia cotteswoldiae* (Upton). $P = 2.4$ laterally, only 1.5 in median deflexion; $N = 11$; grading fair. Cephalopod Bed, Upper Lias (L. Jurassic); Haresfield Beacon, Stroud, Gloucestershire, England. S.M. J. 48668. F, *Nayunella schmuri* (de Verneuil). $P = 3.3$; $N = 25$; grading good. M. Devonian; Eifel, W. Germany. S.M. H. 7607.

A weak dorsal median deflexion then appeared. Soon afterwards the antero-median arc (within the median deflexion) was affected by a weak undulate serial deflexion, which later spread on to the antero-lateral arcs and eventually round on to the postero-lateral arcs. Meanwhile it increased in amplitude. At a fairly late stage it underwent absolute angulation, the crests becoming sharper and the flanks straighter. The final commissure is a zigzag with sharp crests throughout, straight flanks and high relative amplitude anteriorly, curved flanks and well-graded amplitude laterally. It thus resembles the final commissure of many shells in subgroup A. I, although it was derived by a significantly different sequence of events in ontogeny.

Similar zigzags are abundant among the rhynchonellaceans, from at least the Silurian

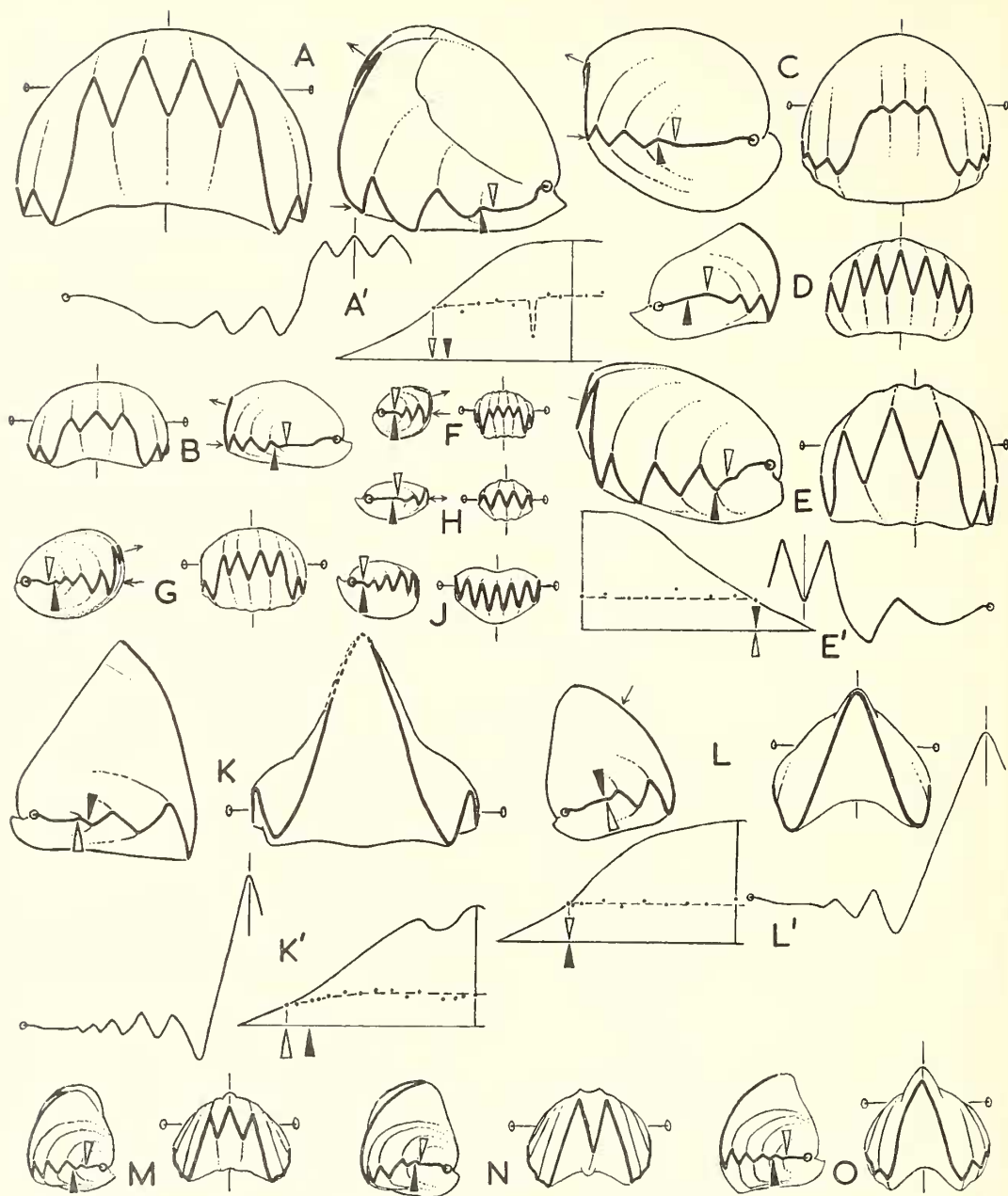
to the Jurassic inclusive (text-fig. 9; Pl. 26; Pl. 27, figs. 1–4), and also occur sporadically in several other superfamilies (text-fig. 10; Pl. 27). The serial deflexion never arose very early in ontogeny, and in some species its appearance was so late that it scarcely produced any clear costae on the valve surfaces (text-fig. 9J; Pl. 27, figs. 1, 2). Its gradual spread on to the lateral arcs can often be seen clearly in the growth-lines (Pl. 26, figs. 1, 3; Pl. 27, figs. 8, 9). On the final commissure, the relative amplitude on the anterior arc may be very high, with angulate crests and straight flanks (Pl. 26, fig. 6); and the zigzag on the lateral arcs may have appropriately curved flanks and graded amplitude (Pl. 26, fig. 5). The grading is often very good or even perfect (text-figs. 9, 10).

Usually there is a dorsal median deflexion, which contains several crests of the zigzag (text-figs. 9A–F, M; 10A, B, D, J; Pl. 26, figs. 1, 2, 6). Rarely there is a similar, but ventral, deflexion (text-fig. 10C, H). In some shells the number of crests within the median deflexion is only three (text-figs. 9N; 10C; Pl. 26, fig. 7). It may even be as low as one, i.e. the median deflexion itself underwent angulation (text-figs. 9K, L, O; 10E, F; Pl. 26, fig. 4). It is interesting to note that one species shows intraspecific variation in this character around a mode of three, with rarer variants with five crests or only one crest in the median deflexion (text-fig. 9M–O). The putative degree of protection within the median deflexion is generally identical with that of the lateral arcs, so that the median deflexion is not apparent on the slit curves (text-figs. 9K', L'; 10A'); but in some shells the zigzag within the median deflexion is distinctly further from the paradigm, having a lower relative amplitude or lower wavelength (text-figs. 9C, F; 10H, J). In a few shells of this subgroup there is no median deflexion (text-figs. 9H; 10G).

In some shells of this subgroup, the costae produced by the zigzag serial deflexion are superimposed on a finer pattern of costellae (Pl. 26, figs. 1, 2; Pl. 27, figs. 5–7). These costellae arose very early in ontogeny, and their early stages may have a close resemblance to the early stages of costae of Group A (compare Pl. 27, fig. 5 with Pl. 21, fig. 4). But unlike those costae, the costellae increased in number (by 'branching' or intercalation), not merely during the earlier stages of growth (Pl. 24, fig. 4), but throughout ontogeny. This suggests that the deflexions which produced the zigzags of Group A may be homologous, not to the deflexions which produced the zigzags of Group B, but to those that produced the costellae on which some of the zigzags of Group B were superimposed.

Subgroup B. II (text-fig. 11; Pl. 28, figs. 1–3): The serial deflexion first arose early in ontogeny, though the crestal number increased throughout ontogeny by the erection of new crests laterally. The earliest crests underwent gradual relative angulation, but all the later (lateral) crests show absolute angulation. A dorsal median deflexion was produced by the relative enlargement of a dorsal median crest of the serial deflexion. (In cumulative terms, the medial costae arise near the umbo of each valve, the lateral costae further away; the median dorsal costa is enlarged anteriorly into a median fold.)

This subgroup is confined to spiriferoids, though it occurs both in the impunctate spiriferaceans of the Silurian and Devonian and in the punctate punctospiraceans at many horizons from the Devonian until the extinction of the group in the Jurassic. The deflection is always conspicuously symmetrical. The progressive erection of new crests throughout ontogeny can easily be seen on the lateral flanks of the valves (Pl. 28, fig. 2). Most of the crests underwent absolute angulation, until on the final commissure a



TEXT-FIG. 9. Zigzags of Subgroup B. I: Rhynchonellacea. All $\times 1.5$. A, A', *Pugnax pugnax* (Martin). A, $P = 2.7$; $N = 19$; grading good; marked growth line shows early median deflexion with very early undulate serial deflexion on anterior arc only. Carboniferous Limestone (L. Carboniferous); Derbyshire, England. S.M. E. 8483. A', commissure trace and slit curve; $P = 1.9$; S.M. E. 8479. B, *Curtirhynchia oolitica* (Davidson). $P = 1.9$; $N = 17$; grading good. Pea Grit, Inferior Oolite (M. Jurassic); Leckhampton Hill, Cheltenham, Gloucestershire, England. S.M. J. 48760. C, *Piarorhynchia cf. juvenis* (Quenstedt). $P = 1.8$ (but only 1.4 in median deflexion); $N = 19$; grading good. Lower Lias (L.

moderately angulate zigzag was formed (text-fig. 11; Pl. 28, figs. 1, 3). Often the grading is rather poor posteriorly (text-fig. 11A, C, E) though it may be good or even perfect (text-fig. 11D, G). Likewise the relative amplitude is usually only moderate, though occasionally it is high (text-fig. 11C). The median crest, which is always dorsal, underwent relative enlargement during ontogeny and became the median deflexion; generally it failed to become angulate and remained unprotected, though occasionally it is fairly angulate (text-fig. 11B, C).

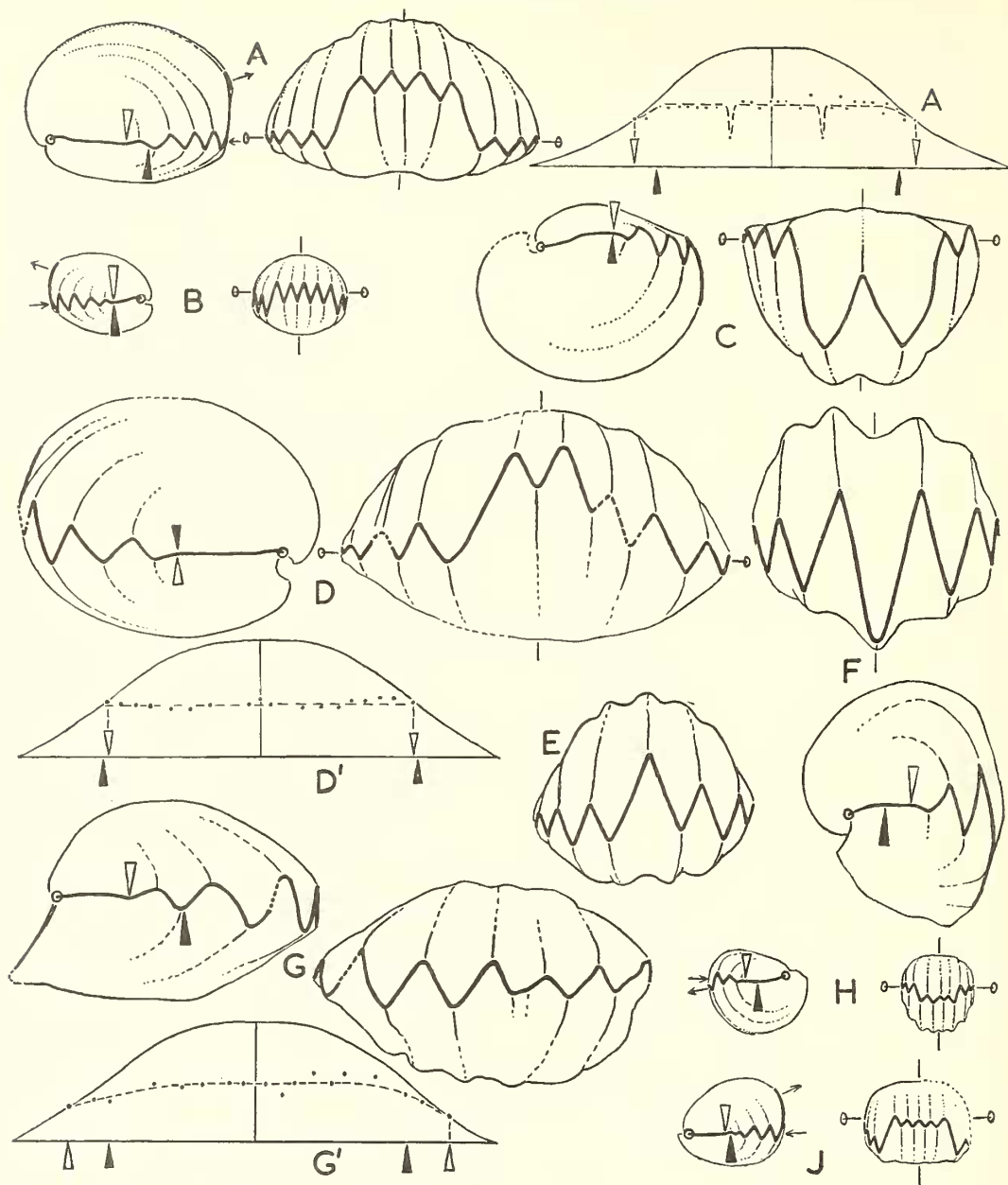
Subgroup B. III (text-fig. 12; Pl. 28, figs. 4, 5): The serial deflexion arose late in ontogeny, and always had a low crestal number (seven or less); it underwent absolute angulation at a late stage. (In cumulative terms, there are only a few broad plicae near the commissure).

This subgroup contains a few miscellaneous species, in all of which the zigzag was produced by the very late absolute angulation of a complex 'fold' incorporating a median deflexion (Pl. 28, figs. 4, 5). The final zigzag is near the paradigm, except that the crests are not highly angulate; the grading is good or even perfect (text-fig. 12).

Accessory crestal protection

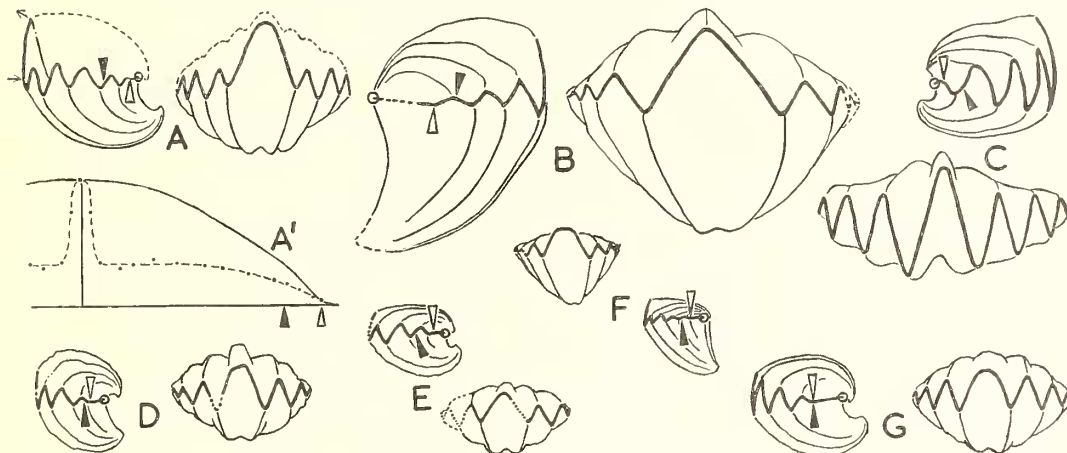
Even in the paradigm, the crests of the zigzag are a deleterious anomaly; however angular they may be, they still allow the passage of 'particles' larger than those passed by the flanks of the slit (text-fig. 2). This anomaly could only be eliminated by placing some accessory structures in these positions. Unless extinct brachiopods possessed organs or tissues entirely unrepresented among living species, only two materials would have been available for this purpose, namely the chitinous *setae* which project from the mantle edge, and the tissue of the mantle edge itself. Both these materials were probably utilized by some brachiopods with zigzag deflexions; but many other zigzag slits probably had no crestal protection.

Jurassic); Tilly-sur-Seulles, Calvados, France. S.M. F. 15992. D, '*Rhynchonella*' *corneliana* Bittner. P = 4; N = c. 19; grading fair. St. Cassianer Schichten (U. Trias); St. Cassian, Bolzano, Italy. (After Bittner 1890, Taf. 3, fig. 18.) E, E', *Rhynchotetra angulata* (Linnaeus). E: P = 3.3; N = 13; grading good; median deflexion slightly asymmetrical. Carboniferous Limestone (L. Carboniferous); Isle of Man. S.M. E. 10186. E', commissure trace and slit curve; P = 3.6. S.M. E. 10165. F, *Monadotoechia monadina* Havlíček. P = 3.5 (2.5 in median deflexion); grading perfect. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 8453. G, *Sphaerirhynchia davidsoni* (M'Coy). P = 3.3; N = 25; grading good. Wenlock Shale (M. Silurian); Daw End, Walsall, Staffordshire, England. S.M. A. 35248. H, '*Rhynchonella*' *attilina* Bittner. P = 2.5; N = c. 9; grading fair. 'Recoarokalk' (M. Triassic); Felsőőrs, Királykút, Hungary. (After Bittner 1890. Taf. 37, fig. 1.) J, *Gnathorhynchia hiostraca* (Buckman). P = 5.0; N = 23; grading perfect. Inferior Oolite (M. Jurassic); Corton Denham, Somerset, England. S.M. J. 6177 (figured Davidson 1884, pl. 19, fig. 19). K, K', *Homoeorhynchia acuta* (J. Sowerby). K: P = 3.5; N = 13; grading good. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 35553. K', Commissure trace and slit curve: P = 4.0. S.M. J. 36233. L, L', *Rhynchonella loxiae* Fischer. P = 2.0; N = 9; grading perfect. 'Portlandien' [= Volgian] (U. Jurassic); Khoroshevo, near Moscow, Russia. S.M. F. 9680. M, N, O, *Homoeorhynchia cynomorpha* (Buckman). M, rare variant with five crests in median deflexion; P = 3.0; N = 22. N, Normal form with three crests in median deflexion; P = 3.0; N = 21. O, Rare variant with one crest in median deflexion; P = 2.5; N = 20. Grading good in all. Upper Freestone, Inferior Oolite (M. Jurassic); the Frith quarry, near Painswick, Gloucestershire, England. S.M. J. 6129-31 (figured Buckman 1895, pl. 14, figs. 2-4).



TEXT-FIG. 10. Zygags of Subgroup B. I: other than Rhynchonellacea. All $\times 1.5$ (except E, F, $\times 1$). A, A', Syntrophiacea: *Parastrophinella reversa* (Billings). $P = 2.0$; $N = 25$; grading good. Ellis Bay formation (U. Ordovician); near Junction Cliff, Anticosti Island, Canada. S.M. A. 9393. B, Syntrophiacea: *Camerella pulchra* Cooper. $P = 3.5$; $N = c. 25$; grading perfect. Wardell formation (M. Ordovician); near Indian Creek, Tennessee. (After Cooper 1956, pl. 114, figs. 30, 31.) C, Pentameracea: *Gypidula acutilobata* (Sandberger). $P = 2.2$; $N = 15$; grading perfect. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 5278. D, D', Dalmanellacea: *Enteleter lamarcki* (Fischer). $P = 2.5$; $N = 19$; grading perfect. Fusulina Limestone (U. Carboniferous); Miatchkowo, Moscow, Russia.

If the mantle tissue was thin and non-erectile (as in living articulate brachiopods) any extensions would have to be supported on extensions of the valves, i.e. on *internal marginal spines*. Such spines could only be accommodated within shells with vertical zones. To reduce to a minimum the drag on the flow of water through the slit, the spines



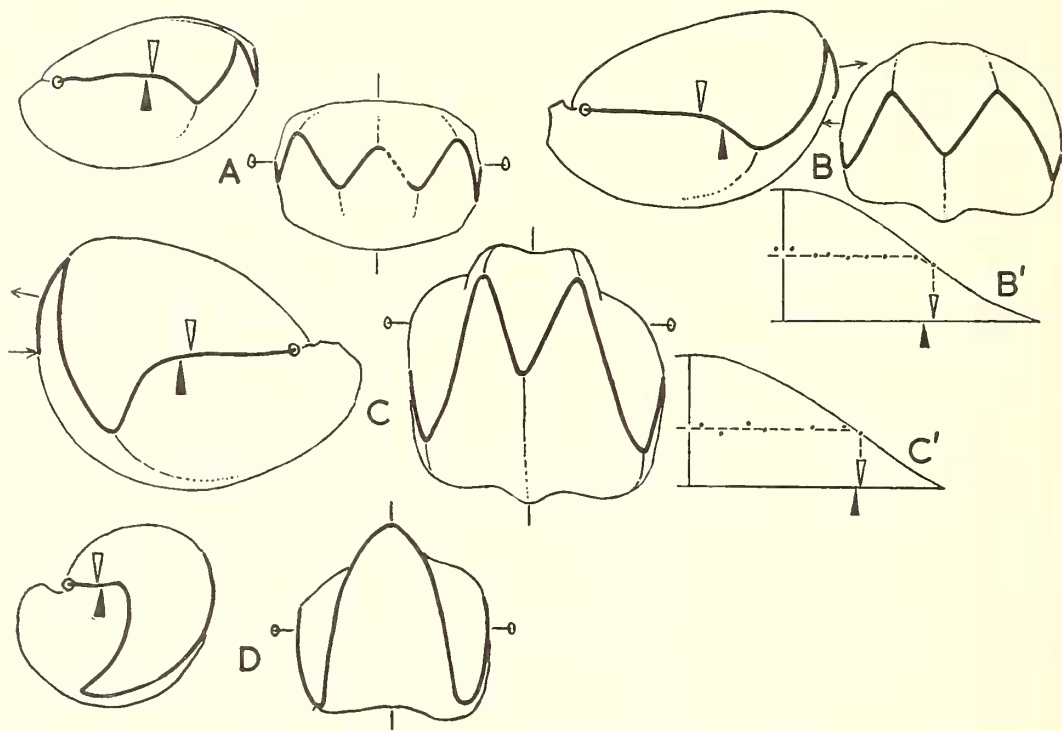
TEXT-FIG. 11. Zigzags of Subgroup B. II: Spiriferoidea. All $\times 1.5$. A, A'. *Spiriferina münsteri* (Davidson): ventral valve only. P = 3.0; N = 21; grading fair. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 36756a. B, *Cyrtina uncinata* (Schafhaeutl). P = 2.0 (less in median deflexion); N = 15; grading good. Kössener Schichten, Rhaetic (U. Trias); Eiseler, Hindelang, W. Germany. S.M. F. 16004. C, *Crenispirifer angulatus* (King). P = 4.0; N = 15; grading fair. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27327/1:2 (figured Stehli 1954, pl. 27, figs. 5, 7). D, *Spiriferellina cristata* (Schlotheim). P = 3.0; N = 15; grading good. Zechstein (U. Permian); Glucksbrunnen, Thuringia, Germany. S.M. E. 16232. E, *Spiriferellina octoplicata* (Sowerby). P = 2.5; N = 15; grading fair. Carboniferous Limestone (L. Carboniferous); Settle, Yorkshire, England. S.M. E. 7241. F, *Cyrtina heteroclita* (Defrance). P = 2.5; N = 17; grading good. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 5283. G, *Howella elegans* (Muir-Wood) (= *Crispella crispa* auctt.). P = 3.0; N = 13; grading perfect. Wenlock Limestone (M. Silurian); Dudley, Worcestershire, England. S.M. A. 26799.

and their sheaths of tissue would need to be as slender as would be consistent with strength: in paradigmatic form their cross-section would be elongated in the direction of flow, i.e. perpendicular to the line of the commissure. To straddle the gape at every crest, the length of the spines would have to be directly proportional to their distance from the hinge-axis. Spines approximating to this paradigm are known in the Silurian

S.M. A. 45955. E, Dalmanellacea: *Eteletes dumblei* (Girty). P = 2.5; N = c. 17; grading good. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27284/1:1 (figured Stehli 1954, pl. 17, fig. 18). $\times 1$. F, Dalmanellacea: *Parenteletes cooperi* King. P = 4.0; grading fair. Gaptank formation (U. Carboniferous); near Gaptank, Glass Mountains, W. Texas. (After Schuchert & Cooper 1932, pl. 24, figs. 11, 13.) $\times 1$. G, G', Orthotetacea: *Meekella striatocostata* (Cox.) P = 2.0; N = 17; grading fair (some anomalies in median arc). U. Carboniferous; Elk County, Kansas. S.M. A. 45954. H, Terebratulacea: *Notothyris minuta* Waagen. P = 2.5 (only 1.7 in median deflexion); N = 17; grading fair. U. Permian; Basleo, Timor. S.M. A. 11548. J, Stenocismatacea: *Stenocisma gregeri* (Branson). P = 2.0 (only 1.5 in median deflexion); N = c. 25; grading good. Coralville formation (M. Devonian); Dodges Creek, Scott Co., Iowa. U.S.N.M.

rhynchonellacean *Sphaerirhynchia wilsoni* (text-fig. 13C, F; Pl. 28, fig. 11; cf. Schmidt 1937), and they reappeared in the Upper Carboniferous rhynchoporacean *Rhynchopora nikitini* (Pl. 24, figs. 6–8).

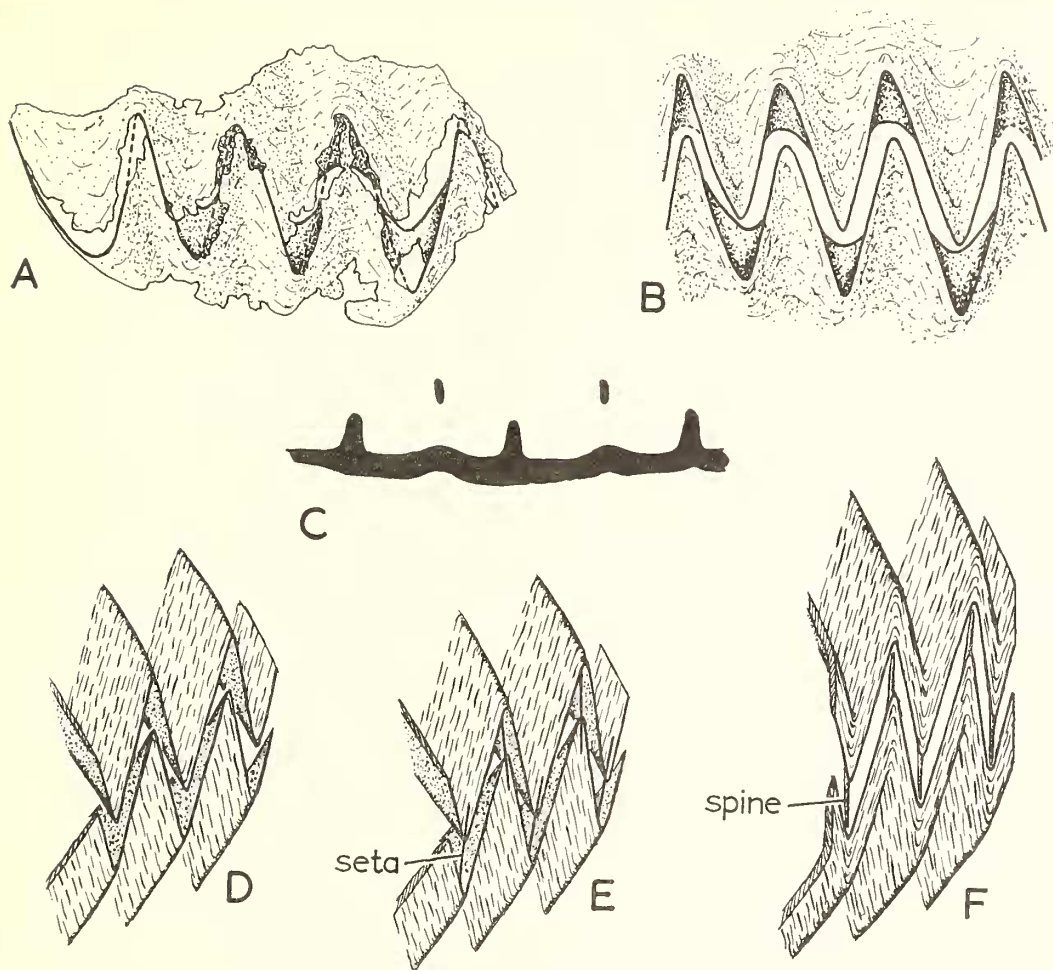
In living articulates, the setae are very slender, and are able to project between the valve edges, even when the valves appear to be tightly closed; and they leave no direct trace in the external form of the shell. Fine setae may therefore have been present in



TEXT-FIG. 12. Zigzags of Subgroup B. III. All $\times 1.5$ (except D, $\times 1$). A, Terebratulaceae: *Antiptychina antiplecta* (von Buch). $P = 2.0$ (only 1.7 medially); $N = 7$; grading perfect. 'Jurakalk' [? Vilsen Schichten] (U. Jurassic); [? Vils], Tirol, Austria. S.M. F. 15998. B, B', Terebratulaceae: *Heimia hollandae* (Buckman). $P = 1.8$; $N = 5$; grading good. Inferior Oolite (M. Jurassic); Bradford Abbas, Dorset, England. S.M. J. 6168 (figured Davidson 1884, pl. xviii, fig. 22). C, C', Terebratulaceae: *Sellithyris upwarensis* (Walker). $P = 2.5$; $N = 5$; grading good. Lower Greensand (L. Cretaceous); Upware, Cambridgeshire, England. S.M. B. 25442. D, Punctospiraceae: *Cyrtiopsis davidsoni* Grabau. $P = c. 5$; $N = 5$; grading probably good. U. Devonian; S. China. (After Grabau 1931–3, pl. 46, fig. 5.) $\times 1$.

many fossil articulates. Stouter and less fragile setae would require special openings at the valve edges. In a few fossil brachiopods, such as the Permian rhynchonellacean *Uncinunellina jabiensis*, small foramina occur at the crests of a zigzag deflexion (Pl. 21, fig. 10). These may be interpreted as the points of emergence of relatively stout setae, which would have provided effective protection at the crests of the zigzag slit.

The setae of living articulates are not erectile. Each lies embedded in the mantle edge, parallel to the inner surface of the valve edge: the orientation of the valve surface thus determines the orientation of the setae. Setae would have been most effective for crestal



TEXT-FIG. 13. Accessory crestral protection of zigzag slits. A, *Parallelelasma pentagonum* Cooper. Fragment of silicified shell showing zigzag on anterior commissure, with internal marginal 'diaphragms' visible where valve-edges are broken. Pratt Ferry formation (M. Ordovician); Pratt Ferry, Alabama. U.S.N.M. 117156f (figured Cooper 1956, pl. 119, fig. 25), $\times 5$. B, The same, with valve-edges restored and gaping narrowly. C, *Sphaerirhynchia wilsoni* (Sowerby). Section of valve-edge parallel to commissure; internal ridges are bases of internal marginal spines; between them the spines from the opposite valve are cut in section. Aymestry limestone (U. Silurian); Sedgley, Staffordshire, England. S.M. A. 30623, $\times 18$. D-F, Diagrams of zigzag valve-edges gaping narrowly, to show zigzag slit unprotected at crests (D), with crestral protection by setae raised on internal 'platforms' (E), and with crestral protection by internal spines (F).

protection if they straddled the gape when the valves opened to the normal extent. But they would not usually have had the correct orientation for this purpose unless the valve edges had a nearly vertical inclination (e.g. on valves with vertical zones). But appropriate thickening of the internal surface of the valves could have changed the orientation of the setae. When the valves closed the setae would have been bent; but when they reopened the setae (which in living species are highly elastic) would have straightened

out and straddled the gape at every crest of the zigzag slit. The amount of thickening required at each crest would depend on the distance from the hinge-axis, but also on the initial inclination of the valve edge. Localized thickenings or *platforms* conforming to this specification are very common in rhynchonellaceans with zigzags of Group A. They occur adjacent to the re-entrants of the zigzag valve edges, and are most readily detected on internal moulds. They are not found on shells of 'immature' form, and were probably secreted once and for all in the final stages of growth. The degree of thickening is conspicuously dependent on the inclination of the valve edges: if the platforms bore setae as postulated, then at one particular degree of opening of the valves each crest of the zigzag slit would have been straddled by one of the setae (text-fig. 13E; Pl. 28, figs. 6, 7, 10). Since these platforms seem to be confined to shells of Group A, it is possible that in this group the crests of the deflexion may have had a one-to-one correspondence with the positions of the setae (as in the serial deflexion of the living *Terebratulina*); and that no such correspondence may have existed in the zigzag deflexions of Group B (as in the serial deflexion of the living *Notosaria*).

Parallelelasma pentagonum is a small pentameracean, with a zigzag of sub-group B. I, found at one horizon and locality in the Middle Ordovician of Alabama. Its most remarkable, and indeed unique, feature is the presence of shelly diaphragms just within the re-entrants of the zigzag valve edges (text-fig. 13A). Each diaphragm is attached near

EXPLANATION OF PLATE 21

Zigzags of Subgroup A. I: Rhynchonellacea.

Fig. 1. *Camarotoechia borealis* (Schlotheim). Postero-dorsal view, showing increase in crestral number during early growth of median arc of serial deflexion. Same specimen as text-fig. 6K, $\times 4.5$.

Fig. 2. *Quadratirhynchia crassimedia* Buckman. Antero-dorsal view of anterior commissure in median deflexion; P = 8. [Middle?] Lias (L. Jurassic); Lyme Regis, Dorset, England. S.M. J. 36893, $\times 3$.

Fig. 3. *Gibbirhynchia gibbosa* Buckman. Left lateral view of median fold, showing gradual loss of crests of serial deflexion on flank of median deflexion. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 35493, $\times 4$.

Fig. 4. *Rhynchotreta cuneata* (Dalman). Right latero-ventral view, showing uniform angularity of crests during ontogeny (relative angulation) and very early origin of serial deflexion. Same specimen as text-fig. 6J, $\times 3$.

Fig. 5. *Stegerhynchus whitii* (Hall). Left lateral view; P = 2.5; N = 23; grading good. Niagara Group (M. Silurian); Waldron, Indiana. S.M. A. 48491, $\times 6$.

Fig. 6. *Globirhynchia subobsoleta* (Davidson). Left postero-lateral view, showing posterior suppression of crests, N reduced from c. 40 to 30; P = 2.7 on final commissure; grading perfect. Oolite Marl, Inferior Oolite (M. Jurassic); Notgrove Station, Gloucestershire, England. S.M. J. 48764, $\times 3$.

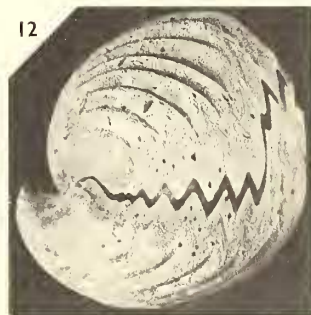
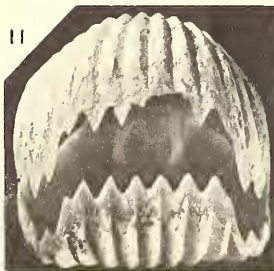
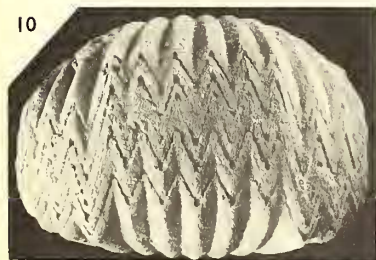
Fig. 7. *Globirhynchia subobsoleta* (Davidson). Right lateral view of 'young' shell, showing poorly graded zigzag. Same specimen as text-fig. 5F, $\times 6$.

Figs. 8, 9. *Russirhynchia fischeri* (d'Orbigny). Right and left antero-lateral views of shell preserved gaping slightly, to show zigzag slit. P = 2.5; N = 20; grading fair. 'Oxfordian' (U. Jurassic); Moscow, Russia. M.C.Z. 6162, $\times 1$.

Fig. 10. *Uncinunellina jabiensis* (Waagen). Anterior view, showing possible setal foramina at crests of zigzag. U. Permian; Basleo, Timor. S.M. A. 11512, $\times 3$.

Fig. 11. Unnamed rhynchonellid. Anterior view of silicified shell, preserved with gape much greater than amplitude of zigzag (crura visible internally). L. Callovien (U. Jurassic); Chatillon-sur-Seine, Côte d'Or, France. U.S.N.M. acc. 195551, $\times 3$.

Fig. 12. Rhynchonellid as fig. 11. Right lateral view of silicified shell, preserved gaping with narrow zigzag slit; note vertical zone, on which serial deflexion has no cumulative expression (i.e. no costae). Locality as fig. 11, $\times 3$.



the edge of the inner surface of the valve; growth-lines on the diaphragms (see Cooper 1956, pl. 121, fig. 1) indicate that they were built up by accretion at the free edges, presumably by secretion by the mantle cells at or just within the mantle edge. Cooper terms this structure 'a very efficient straining device for the food-bearing currents' (1956, p. 612), but does not explain this interpretation in detail. But if the valves gaped apart giving a zigzag slit, the diaphragms would have straddled the crests of the slit immediately inside the edges of the valves (text-fig. 13B), and thus would have provided effective protection at the crests—but only at the expense of a considerable reduction in the total area of the slit. The inherent inefficiency of this variety of crestal protection may account for its extreme rarity.

Zigzag deflexions in oysters

By far the closest analogues to zigzag deflexions in fossil brachiopods are found in certain oysters (Pl. 29). Although they belong to a different phylum, oysters possess in common with brachiopods a hinged bivalved shell which, on gaping open, reveals inhalant and exhalant apertures bordered by sensitive mantle edges. Zigzag deflexions have probably arisen many times independently in the history of the oysters, and are known at several horizons from the Triassic onwards. Zigzags of highly paradigmatic form can often be found: they have a high degree of protection and sharply angulate crests; the amplitude is well graded, with straight flanks on arcs parallel to the hinge-axis (Pl. 29, figs. 2, 4, 5) and curved flanks towards the hinge-axis (Pl. 29, figs. 1, 3, 7); and the grading is progressively improved in the final stages of ontogeny by posterior crestal suppression (Pl. 29, fig. 1: strictly speaking, in lamellibranch orientation, the crestal suppression should be termed *dorsal*). Even when the commissure plan became crescentic during ontogeny, the grading was clearly correlated with perpendicular distance from the hinge-axis, thus ensuring a slit of uniform width.

THE INTERPRETATION OF ZIGZAG DEFLEXIONS

Zigzag deflexions and the protective paradigm. The foregoing survey shows that zigzag deflexions in brachiopods—and oysters—approximate to the paradigm for protective devices. The approximation may be very close or only moderate; but all these deflexions show an unambiguous *approach* towards the paradigm, which justifies the assertion that they would have been capable of functioning as moderately efficient or even (in some instances) highly efficient protective devices. Indeed zigzag deflexions must *necessarily* have had this function; for whenever the valves gaped apart the zigzag slit must necessarily—by virtue of its form—have conferred relative protection on the gape. Any interpretation of zigzags that questions their adaptive status (e.g. a 'phylogerontic' explanation) is therefore inadmissible.

The specification of the paradigm is rather rigidly determined by the geometry of a zigzag and of a hinged bivalved shell. Any efficient protective zigzag must conform to this specification, in whatever brachiopod (or oyster) species it occurs. Consequently it is *inherently* probable that zigzags were evolved many times in the history of the Brachiopoda. This is probably a factor contributing to the complex evolutionary history of the phylum.

Nature of the 'harmful particles'. All roughly equidimensional particles would have an effect similar to perfect spheres. But this assumes (following Schmidt) that the zigzag slit would have been 'protective' by being a straining device: i.e. that while the valves remained open, the zigzag slit would sort approaching particles into two classes on the basis of their size, rejecting one class and accepting the other. Some analogous straining devices are known in other animals. The inhalant apertures of the lamellibranch *Tivela stultorum* Mawe and the gastropod *Turritella communis* Risso are covered by meshes (formed from pinnate tentacles), which fulfil a straining function by excluding sand grains and admitting the smaller food particles (Weymouth 1923, p. 11; Graham 1938, p. 454). As an example from an entirely different animal, the slit between the jaws of the filter-feeding flamingo *Phoeniconaias minor* (Geoffroy) is protected by a row of regularly spaced 'marginal hooks' which act as a straining device (Jenkin 1957). But much closer

EXPLANATION OF PLATE 22

Zigzags of Subgroup A. 1: Rhynchonellacea.

Fig. 1. *Tetrarhynchia tetrahedra* (Sowerby). Anterior view, showing development of zigzag within median deflexion; angulation predominantly relative, but absolute at first. $P = 4.0$ on final commissure (foreshortened). Middle Lias (L. Jurassic); King's Sutton, Oxfordshire, England. S.M. J. 46810, $\times 4.5$.

Fig. 2. *Tetrarhynchia tetrahedra* (Sowerby). Right lateral view, showing development of graded zigzag; angulation predominantly relative, but absolute at first. Locality as fig. 1. S.M. J. 46808, $\times 4.5$.

Fig. 3. *Globirhynchia subobsoleta* (Davidson). Left postero-lateral sectors, showing gradual posterior suppression of crests and consequent improvement of grading. Same specimen as Plate 21, fig. 6, $\times 9$.

Fig. 4. *Globirhynchia subobsoleta* (Davidson). Right antero-lateral arc, showing flank of zigzag lengthened to form flank of median deflexion, without significant change in orientation. Same specimen as text-fig. 5A-C, $\times 6$.

Fig. 5. *Globirhynchia subobsoleta* (Davidson). Right lateral view, to show relative angulation of zigzag and posterior suppression of crests from $N = 39$ to $N = 29$; $P = 2.5$; grading good on final commissure. Locality as text-fig. 5A-F. S.M. J. 48765, $\times 6$.

Fig. 6. *Prionorhynchia serrata* (Sowerby). Anterior arc of commissure, $P = 3.0$. [Middle] Lias; Ilminster, Somerset, England. S.M. J. 35742, $\times 4.5$.

EXPLANATION OF PLATE 23

Zigzags of Subgroup A. 1: figs. 1-4 Rhynchonellacea; figs. 5-8 other superfamilies.

Fig. 1. *Quadratrhyndia crassimedia* Buckman. Left postero-lateral view, to show graded zigzag developed from early serial deflexion; $P = 8$; $N = 53$. Locality as Plate 21, fig. 2. S.M. J. 36892, $\times 3$.

Fig. 2. *Gibbirhynchia gibbosa* Buckman. Left lateral view, to show graded zigzag ($P = 5.0$) developed from early serial deflexion, with crestal suppression (N reduced from c. 63 to 37). Same specimen as Plate 21, fig. 3, $\times 6$.

Fig. 3. *Gibbirhynchia gibbosa* Buckman. Right postero-lateral view, to show undulate crests persisting posterior to ideal suppression point. Locality as Plate 21, fig. 3. S.M. J. 35487, $\times 6$.

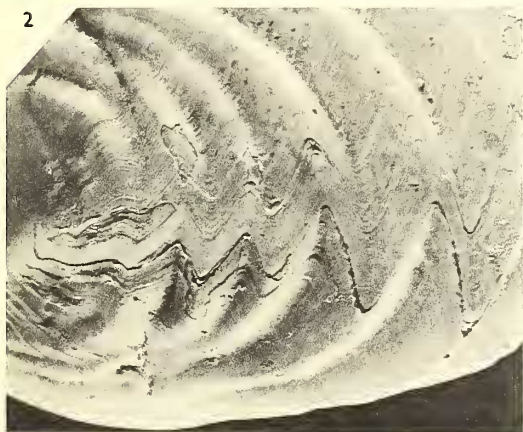
Fig. 4. *Lepidocyclus capax* (Conrad). Left lateral view, to show development of graded zigzag by relative angulation. Same specimen as text-fig. 6L, $\times 4.5$.

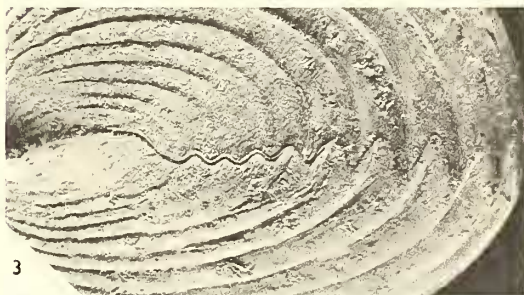
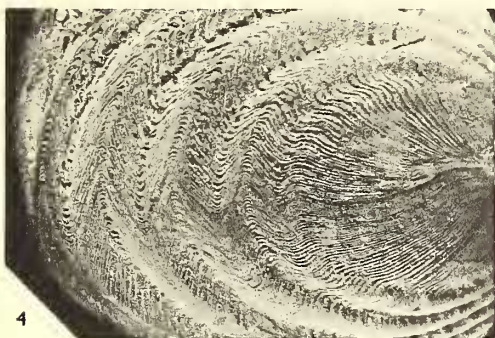
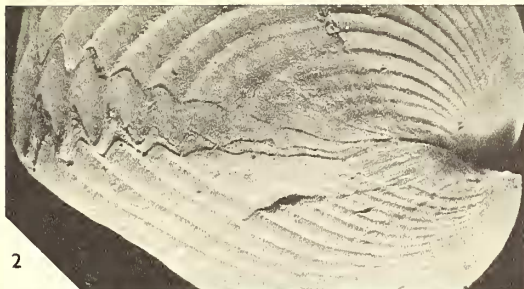
Fig. 5. Orthacea: *Platystrophia crassa* (James). Right antero-lateral view, to show zigzag modified by posterior median deflexion. Same specimen as text-fig. 7E, $\times 3$.

Fig. 6. Terebratulacea: *Eudesia cardium* (Lamarck). Left postero-lateral sectors, to show development of graded zigzag by posterior crestal suppression (note punctate shell-structure). Same specimen as text-fig. 7J, $\times 6$.

Fig. 7. Terebratulacea: *Ismenia pectunculoides* (Schlotheim). Left lateral view, to show posterior crestal suppression. Same specimen as text-fig. 7M, $\times 3$.

Fig. 8. Punctospiracea: *Hustedia mormoni* (Marcou). Left postero-lateral view, to show development of zigzag from very early serial deflexion (note strophic hinge). Same specimen as text-fig. 7L, $\times 9$.





analogues are provided by the oysters with zigzag deflexions; and these suggest a significantly different conception of the 'protection' that might be given by a zigzag slit in a fossil brachiopod. *Ostrea crista-galli* Linnaeus and *Pycnodontes lyotis* (Linnaeus) both occur in tropical waters of the Indo-Pacific region (Thomson 1954). *O. crista-galli* often has a highly developed zigzag deflexion (Pl. 29, figs. 6, 7). *P. lyotis* has a rather less perfect zigzag, but is relatively accessible on the Great Barrier Reef. When feeding normally the valves do not gape far apart, so that a relatively narrow zigzag slit is formed (especially on the inhalant aperture: on the exhalant the deflexion generally remains undulate). The mantle edges lining the slit are sensitive (in this species, unlike many others, they are not modified into sensitive tentacles to guard the gape). If a swimming animal or other object touches the side of the slit, the valves immediately snap shut, by a rapid contraction of the 'quick' portion of the adductor muscle. Thus the zigzag slit is not a passive straining device, but protects the animal with an active and highly sensitive *warning device*.

Although no living brachiopods possess zigzag deflexions, their physiology suggests a similar interpretation. The mantle edge is highly sensitive both to tactile and to chemical stimuli. All the nerve fibres that radiate outwards across the mantle from the central ganglia terminate within the extreme marginal zone of the mantle, and the sensitivity of the mantle is limited to this narrow zone. When the mantle edge is stimulated, the valves are immediately snapped shut by a very rapid contraction of the 'quick' striated posterior adductor muscles (Rudwick 1961*b*). If, as it is reasonable to assume, all articulate brachiopods have possessed mantle edges with similar properties, the acquisition of a zigzag deflexion could represent the further development of this warning device.

This means that a zigzag slit could protect a brachiopod from much smaller 'harmful particles' than Schmidt's hypothesis implied. One such particle might penetrate the slit without touching or stimulating the mantle edge on either side; but a suspension of many small particles would be more likely to be detected, since at least a few of them might touch the mantle edges (or at least approach closely enough to be detected chemically). This would accord well with the rejection mechanisms of living brachiopods: occasional isolated particles are ejected with scarcely any disturbance of the filter-feeding, but a thick suspension (e.g. of sand grains or mud) brings a more radical rejection mechanism into operation, and may seriously interrupt the filter-feeding on part or all of the lophophore (see Rudwick 1962*b*, pp. 609–11). The efficiency of a zigzag slit for detecting small suspended particles could be expressed by the same 'degree of protection' as that defined in the original specification (text-fig. 1A, MN/XY). Thus whatever the exact nature of the 'harmful particles' that a fossil brachiopod might have encountered, a zigzag slit could have provided effective protection against them: the paradigmatic specification remains the same, and can be expressed in terms of idealized spherical particles, even though no such particles may ever have existed.

There is some doubt, however, whether in fact a narrow zigzag slit represents the normal degree of opening of the valves. For example, in one rhynchonellacean species (preserved by silicification) some specimens show a good zigzag slit between the valves (Pl. 21, fig. 12), but others show that the valves could gape much more widely without breaking the hinge (Pl. 21, fig. 11). In this and many other species, especially those with a rather high crestral number, it is clear that the zigzag deflexion would not have

produced a zigzag slit unless the valves opened only very slightly (Pl. 28, figs. 6–9). This is unlikely to have been the normal degree of opening: such narrow apertures would have created great resistance to the flow of water, and would have been much smaller than those in living brachiopods, in which the valves normally gape apart almost as widely as the hinge-structure allows.

But, as a warning device, a zigzag slit would have been most important in the early stages of reopening of the shell. During the slow reopening of the shell, living brachiopods appear to ‘test’ the environment to determine whether the factor that provoked the original closure still persists. (If it does persist, the shell may be snapped shut again at once, long before the normal degree of opening has been attained.) Thus any brachiopod with zigzag valve-edges would have had a heightened ‘degree of protection’ at least during this crucial early phase in the reopening of the shell; and the nearer the paradigm (i.e. the higher the value of P and the lower the value of N), the longer the period of reopening during which the zigzag would have been effective. In some shells with highly paradigmatic zigzags, the apertures may have retained their form as zigzag slits even when the valves were gaping apart to the fullest extent.

Zigzag deflexions and current-systems. The protection conferred by a zigzag slit is commonly uniform all round the commissure (apart from imperfect grading in the

EXPLANATION OF PLATE 24

Zigzags of Subgroup A. I: other than Rhynchonellacea.

Fig. 1. Athyracea: *Trematospira salteri* (Davidson). Left antero-lateral view, to show graded zigzag in lateral arc, with poorer zigzag of low wavelength in median deflexion. Same specimen as text-fig. 7G, $\times 6$.

Fig. 2. Orthacea: *Platystrophia cypha* (James). Anterior view, to show suppression of crests on flanks of median deflexion. Same specimen as text-fig. 7D, $\times 3$.

Fig. 3. Orthacea: *Platystrophia ponderosa* Foerste. Right postero-lateral view, to show crestral suppression. ‘Hudson River Group’ (U. Ordovician); Cincinnati, Ohio. S.M. 45745, $\times 2$.

Fig. 4. Terebratulacea: *Eudesia cardium* (Lamarck). Postero-dorsal view, to show early increase in crestral number of serial deflexion. Same specimen as text-fig. 7J, $\times 6$.

Fig. 5. Terebratulacea: *Choristothyris plicata* (Say). Right postero-latero-dorsal view, to show early origin of serial deflexion, relative angulation, and posterior crestral suppression. Same specimen as text-fig. 7K, $\times 4.5$.

Figs. 6–8. Rhynchoporacea: *Rhynchopora nikitini* Tschernyschew. Left lateral, right lateral, and anterior views of an internal mould, showing graded zigzag with internal spines (showing as grooves on mould) at every crest; note also moulds of punctae. Same specimen as text-fig. 7A, $\times 6$.

EXPLANATION OF PLATE 25

Zigzags of Subgroup A. II: Rhynchonellacea.

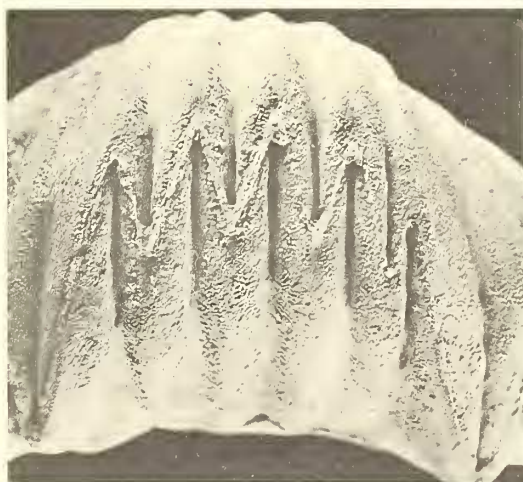
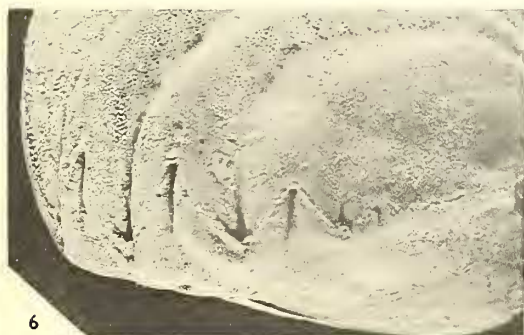
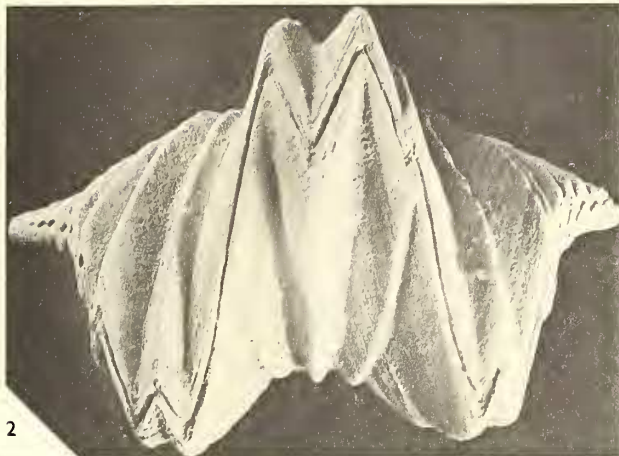
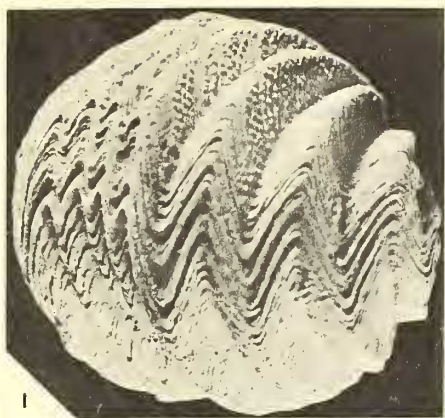
Figs. 1, 2. *Rimrhynchia anglica* (Rollier). Left lateral views, to show early serial deflexion of large crestral number, crestral reduction initiated antero-laterally and spreading medially and laterally, and final production of graded zigzag. Same specimen as text-fig. 8B. Fig. 1, $\times 3$; fig. 2, $\times 6$.

Fig. 3. *Rimrhynchia anglica* (Rollier). Right antero-latero-ventral view, to show crestral reduction on antero-lateral arc, failing to spread into median deflexion. Same specimen as text-fig. 8D, $\times 6$.

Fig. 4. *Rimrhynchia anglica* (Rollier). Right postero-latero-dorsal view, to show crestral reduction on antero-lateral arc, failing to spread to postero-lateral arc. Same specimen as text-fig. 8D, $\times 6$.

Fig. 5. *Cyclothyris antidiplotoma* (Buvignier). Antero-dorsal view, to show fairly early crestral reduction. Same specimen as text-fig. 8A, $\times 3$.

Fig. 6. *Naynella schmri* (de Verneuil). Antero-ventral view, to show late crestral reduction. Same specimen as text-fig. 8F, $\times 4.5$.

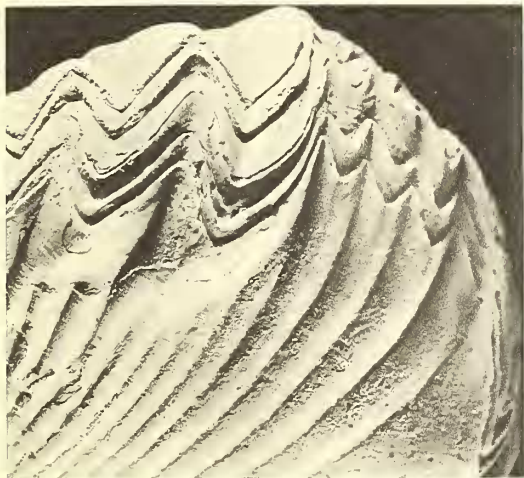




2



1



3



5



6



4

posterior arcs). Therefore the inhalant and exhalant apertures must have shared the same degree of protection, wherever they were situated. This cannot be explained by assuming that the apertures were variable or interchangeable in position: for in living species they are constant in position, apart from slow ontogenetic changes (Rudwick 1962*b*); and reversal of the current-system, and hence of the nature of the apertures, occurs only as a rare and exceptional rejection mechanism (Atkins 1960, p. 470; Rudwick 1962*b*, p. 611). But, in at least some living species, the valves habitually gape apart even when the lophophore is inactive and no currents are flowing (Atkins 1959, p. 130). For species with this habit, an equal degree of protection on all the apertures might be advantageous.

But in a number of zigzags it has been noted that the degree of protection is distinctly poorer on the median arc—whether or not that arc is modified by a median deflexion—than on the lateral arcs. A similar poorly zigzagged arc on the living oyster *Pycnodonia hyotis* represents the position of the exhalant aperture. By analogy, the poorly protected median arc of a brachiopod may represent the site of a median exhalant aperture, which was often deflected dorsally or ventrally away from a pair of lateral inhalant apertures. This system of apertures is almost universal in living articulate brachiopods, apart from early growth-stages and a few very small species (Rudwick 1962*b*). If this inference is correct, it gives evidence for the reconstruction of the current-system, independently from that given by the structure and orientation of the lophophore and its skeletal supports. For example, if a poorly protected median deflexion in a spiriferoid represents a median exhalant aperture, the exhalant current must have emerged medially from the interior of the spiralia (Rudwick 1960), not laterally from the exterior of the spiralia (Williams and Wright 1961). A lower degree of protection on the exhalant aperture would not have been disadvantageous to a species in which the valves never gaped apart except when the lophophore was operative: this habit, like the converse, is known in some living species (Rudwick 1962*b*, p. 607).

A possible anomaly in this interpretation is the existence of a few shells, of which the Carboniferous rhynchonellacean *Pugnax acuminatus* (Martin) is perhaps best known, in which the median deflexion alone underwent absolute angulation, leaving the lateral arcs apparently unprotected. It is possible, though unlikely, that the apertures were reversed in these species. It is more probable that the lateral apertures were equipped with more effective rejection mechanisms than the median aperture (viz. the cilia on the filaments, rather than the mantle cilia), so that protection by a narrowed slit was more necessary on the median than on the lateral apertures.

Ontogeny of zigzag deflexions. All zigzag deflexions developed gradually during ontogeny, showing a progressively closer approximation to the protective paradigm. On most shells, the zigzag was close to the paradigm only in the later growth stages and, above all, on the final commissure of the 'mature' shell. Since the rate of growth of living brachiopods seems to decrease progressively throughout life (Rudwick 1962*a*), the 'final' stages of growth may actually represent a large part of the total life-span. But whatever the proportion of time involved, it is clear that good protective zigzags were in general confined to the later part of the life-span. But this does not imply that the protection developed suddenly *ex nihilo* at some point in ontogeny, since the protection given by a zigzag slit is only an extension and improvement of that given by valve edges of any form (if they are lined with sensitive mantle edges). Protection as such would have existed throughout life, but would not have reached a high degree until the later